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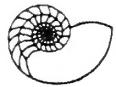
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CONTENTS

Maurício Romulo Fernandes Juan Francisco Araya	New species and records of Triphoroidea (Gastropoda) from Chile	1
Kristine Greke	New species and record of <i>Diplommatina</i> Benson, 1849 (Gastropoda: Diplommatinidae) from Java, Indonesia	14
Kazutaka Amano	A Paleocene species of <i>Procardia</i> (Bivalvia: Anomalodesmata: Parilimyidae) from the Katsuhira Formation in Urahoro Town, eastern Hokkaido, Japan	22
Tomoki Kase Shinji Isaji Yolanda M. Aguilar Steffen Kiel	A large new <i>Wareniconcha</i> (Bivalvia: Vesicomyidae) from a Pliocene methane seep deposit in Leyte, Philippines	26
Notice	30	



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New species and records of Triphoroidea (Gastropoda) from Chile

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ABSTRACT

The present study aims to describe specimens of Triphoroidea recently sampled from Chilean waters, with two species from the northern continental shelf and one from the Juan Fernandez Archipelago. *Cerithiopsis eiseni* Strong and Hertlein, 1939, originally described from western Panama, has its protoconch, operculum and radula illustrated for the first time. *Monophorus monocelha* new species is recognized by having a very thick shell; yellowish protoconch and brown teleoconch; median spiral cord emerging between the sixth/seventh whorl of teleoconch; a brown mark between the eyes; and radular formula 4-1-1-4. *Inella basalis* (Odhner, 1922) new combination is recorded almost a century after its original description, including data on intraspecific variation in adult size, shape of protoconch, number of axial ribs on teleoconch, and number of basal and supranumerical cords. *Cerithiopsis eiseni* and *Monophorus monocelha* new species share very thick shells and narrow apertures, suggesting a convergent defensive mechanism against predation.

Additional Keywords: Triphoridae, Cerithiopsidae, taxonomy, marine gastropods

INTRODUCTION

The superfamily Triphoroidea has species with high-spired and comparatively small shells, with the adult shell usually being less than 10 mm long (Wells, 1998). Their specialized feeding mode on sponges produced an amazing diversity of radular morphologies, especially in the left-coiled triphorids (Marshall, 1983). Three families of Triphoroidea are currently recognized: Newtoniellidae is often present in the deep sea, while Triphoridae and Cerithiopsidae are usually found in shallow and tropical/temperate waters (Fernandes and Pimenta, 2017a). Triphoridae and Cerithiopsidae belong to the group of the “Big Five”, representing the five most

species-rich families of marine gastropods in the world (Bouchet et al., 2002; Albano et al., 2011).

Most taxonomic works of Triphoroidea from the eastern Pacific were published from mid-19th to mid-20th centuries (e.g., Adams, 1852; Bartsch, 1907, 1911; Baker, 1926; Baker et al., 1938), with the most recent ones dating back to almost four decades (e.g., DuShane and Draper, 1975). The majority of these species was described from the northeastern Pacific, with few studies covering the Southern Hemisphere. Species were described almost exclusively based on shells, with spare exceptions including a drawing of the head-foot in one species (DuShane and Draper, 1975), and the investigation of the reproductive system of three species (Houston, 1985). The knowledge about other important structures (such as radula and operculum) for the taxonomy of this superfamily in the eastern Pacific is lacking.

In Chilean waters, three species of Cerithiopsidae and 11 of Triphoridae were recorded from Easter Island (Odhner, 1922; Rehder, 1980; Raines, 2002), in addition to one species of each family from the Juan Fernandez Archipelago (Odhner, 1922). With the exception of *Cerithiopsis magellanica* Bartsch, 1911, described from a locality near Punta Arenas, and the Miocene fossil *Cerithiopsis pyrgiscus* (Philippi, 1887), only larval forms of both families were reported from coastal Chile (Romero and Valdebenito, 2002), in addition to beach-worn or empty shells without specific determination (Marincovich, 1973; Guzmán et al., 1998). Two Newtoniellidae species were reported to occur in the continental shelf of Chile: *Ataxocerithium pullum* (Philippi, 1845), which has a mainly magellanic distribution and was recorded as far north as Chiloé Island in the Pacific (Cárdenas et al., 2008), and *Eumetula michaelensi* (Strebel, 1905), from the Straits of Magellan (Strebel, 1905).

The objective of the present study is to evaluate the taxonomy of recently sampled species of Triphoroidea from Chilean waters, with two species from the continental shelf of northern Chile and one from the Juan Fernandez Archipelago.

MATERIALS AND METHODS

Part of the material was collected by trawls in the Juan Fernandez Archipelago, a set of three volcanic islands situated 670 km off continental (central) Chile, in 2004. Hand-collected specimens were obtained from Caldera, northern coastal Chile, in 2012 and 2016, by the second author. In the last case, some live specimens were found among sponges.

Color photographs were obtained with a Zeiss AxioCam ICe5 camera on a Zeiss Discovery.V20 stereomicroscope, and scanning electron microscope (SEM) images taken with a JEOL JSM-6390LV. Shell descriptions followed Fernandes and Pimenta (2015), and were solely based on the examined material. For specimens with soft parts, the shell was photographed and cracked, then the external morphology was photographed, and internal hard structures (operculum, jaw and radula) extracted following Geiger et al. (2007). When necessary to avoid confusion, cusps of radular teeth were numbered from the innermost cusp (cusp 1), close to the rachidian/central tooth, toward the outermost cusp, distant from the central tooth; cusps of central teeth are numbered from left to right when many cusps are present. The number of specimens or shells from each lot is indicated between square brackets, and 'd' refers to specimens partly or completely destroyed for the study of internal hard structures. As a consequence of the recent fire at MNRJ on September 2018 (Zamudio et al., 2018), only the type material of the new species herein described was saved, whereas the ordinary material listed in this study and stored at MNRJ was unfortunately lost.

Acronyms: CAS: California Academy of Sciences, San Francisco, USA; MNRJ: Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; USNM: National Museum of Natural History, Smithsonian Institution, Washington, USA; SBMNH: Santa Barbara Museum of Natural History, Santa Barbara, USA.

SYSTEMATICS

Subclass Caenogastropoda Cox, 1960

Superfamily Triphoroidea Gray, 1847

Family Cerithiopsidae Adams and Adams, 1853

Genus *Cerithiopsis* Forbes and Hanley, 1850

Type Species: *Cerithium tuberculare* Montagu, 1803, by original designation. Recent, Europe.

***Cerithiopsis eiseni* Strong and Hertlein, 1939**

(Figures 1–18)

Cerithiopsis eiseni Strong and Hertlein, 1939: 216, pl. 20, fig. 6; Hertlein and Strong (1955: 135, not figured).

Type Locality: Bahia Honda, 5–16 m, Veraguas, western Panama.

Type Material: Holotype: CAS 65665. The additional shells listed in Strong and Hertlein (1939) are also stored at CAS. Although they do not yet have lot numbers (Christina Piotrowski, pers. comm.), they can be regarded as paratypes (ICZN, 1999: article 72.4.1).

Material Examined: MNRJ 23163, 27°05'15" S, 70°51'29" W, Calderilla beach, under sunken rocks at very low tide, Caldera, Region of Atacama, J. F. Araya and M. Araya coll., February 9, 2016, 5 specimens, 3 d.

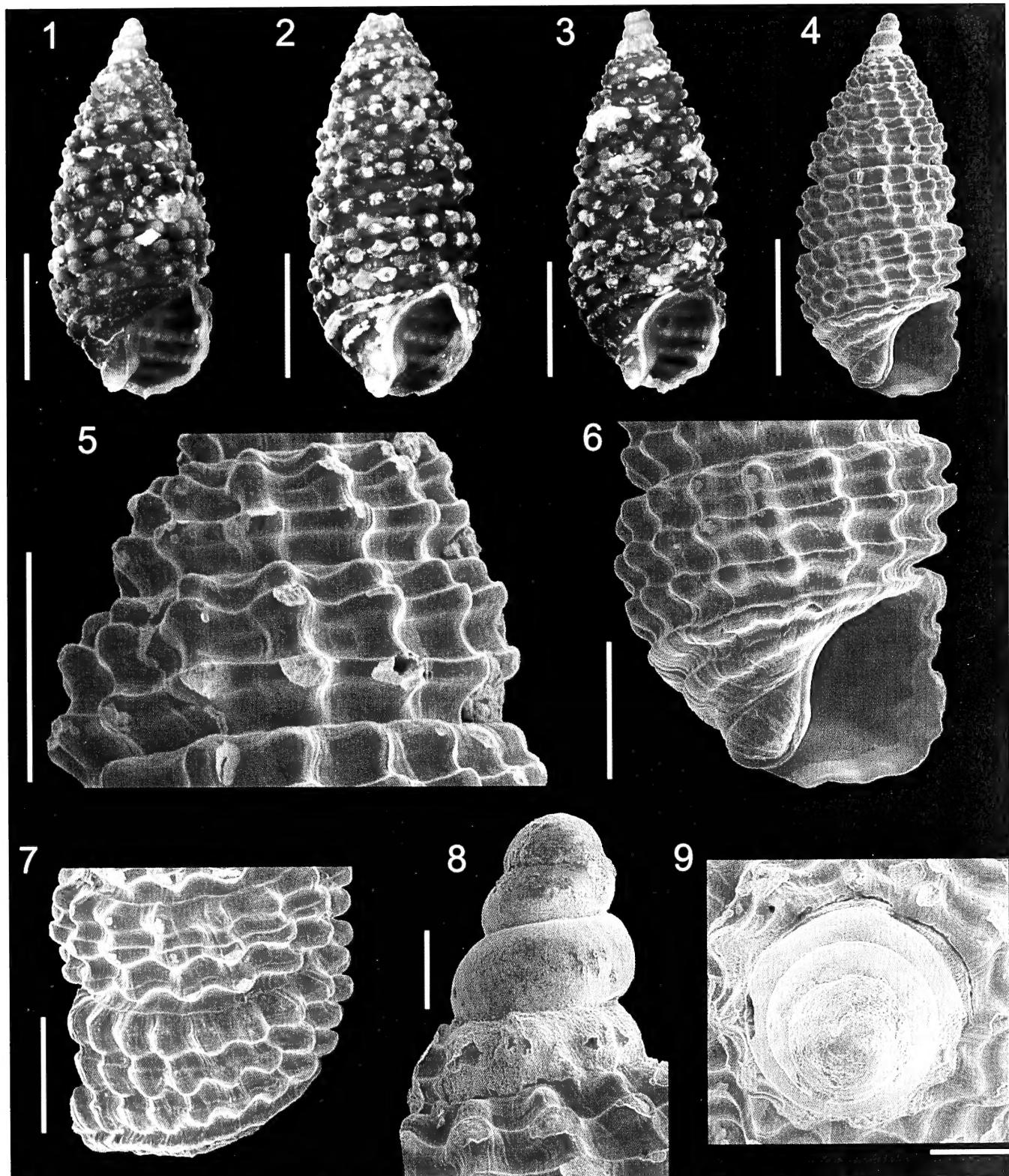
Description: Shell: dextral, ovoid to slightly elongate, very thick, concave profile, up to 3.4 mm long, 1.4 mm wide, ratio length/width 2.3 to 2.5. Protoconch multispiral, conical/cylindrical but slightly mammillated, 0.35 mm long, 0.30 mm wide; 3.5 much convex whorls, clear transition between protoconch and teleoconch; embryonic shell dome-shaped; larval shell mainly smooth, except by very fine, near orthocline to slightly prosocline, axial threads covering entire length of last whorl. Teleoconch with up to six whorls; two main spiral cords (median and abapical) at beginning, with third one (adapical) very close to median one, gradually developing and reaching nearly same size of other cords on fifth whorl; on body whorl, mean distance between cords is 1.1–1.4× higher than mean width of cords; 15 to 19 orthocline to slightly prosocline axial ribs on fifth whorl; rounded (particularly on adapical and median cords) to slightly elliptical (particularly on abapical cord) nodules of large size; distinct suture, with small, partially hidden sutural cord; thick, wavy to weakly nodulose subperipheral cord, two smooth to slightly wavy basal cords, adapical one considerably thicker; small, elliptical aperture, 0.72–0.74 mm long, 0.50–0.52 mm wide, ratio length/width 1.4; anterior canal very short, wide, completely open, 0.16–0.18 mm long, 0.19–0.23 mm wide; posterior canal as small notch, 0.11–0.12 mm long. Teleoconch with reddish-brown to dark-brown background, spiral cords dark brown with yellowish nodules, protoconch yellowish to light golden.

External Morphology of Soft Parts: Color cream-white, five to six light brown stripes mantle cavity roof; adapical portion of half to one whorl posterior to head covered by several small black dots.

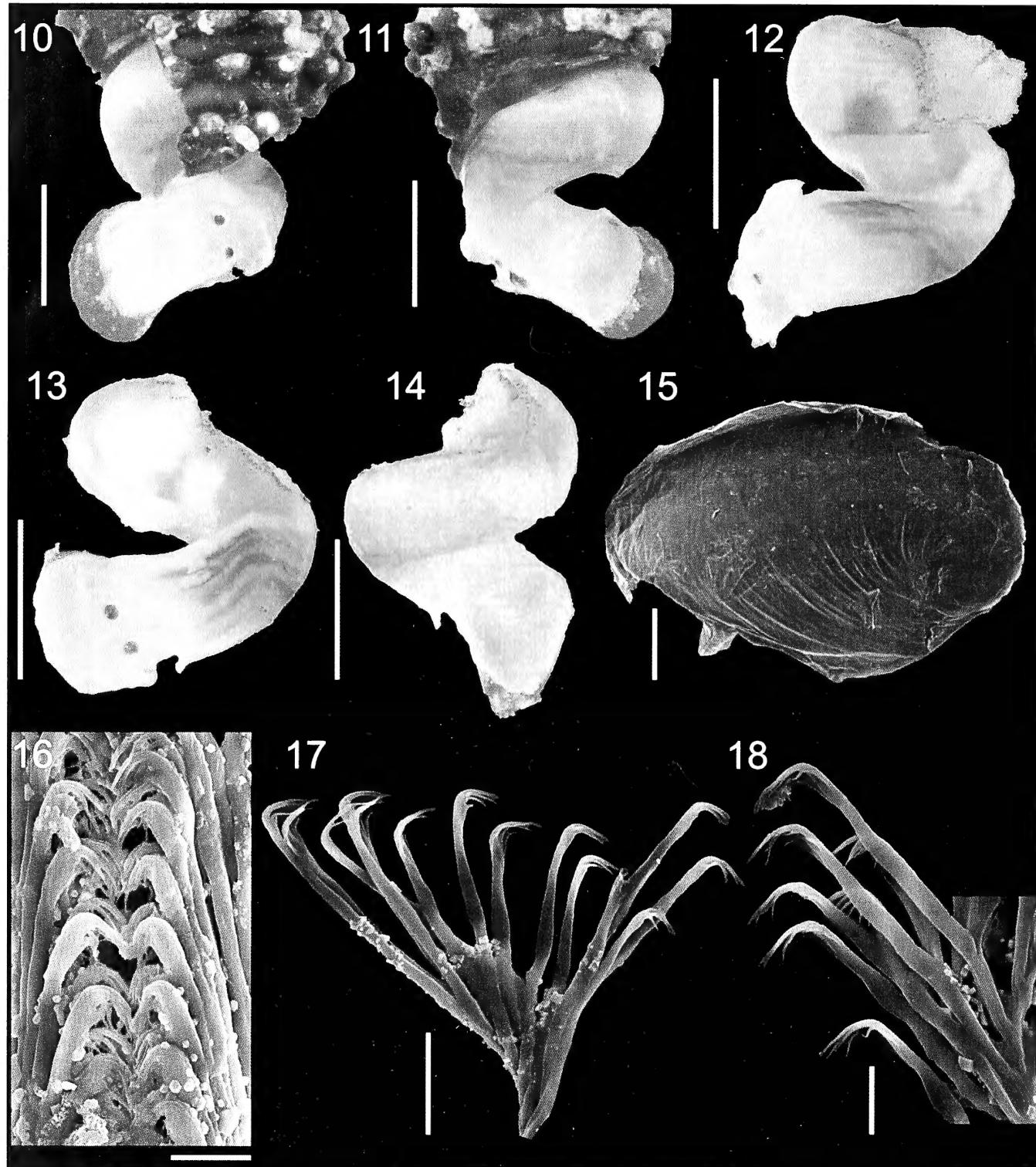
Operculum: Elliptical, thin, semi-transparent, paucispiral, 2.5 whorls, nucleus eccentric, displaced 72% from center toward margin; maximum length of operculum exceeds diameter of opercular disc by 23% to 60% on anterior edge.

Radula: Only marginal teeth were discernible, 32.1–38.6 μm long, usually bearing seven elongated and curved cusps on distal portion of teeth (occupying 11% to 25% of their total length, positioned almost perpendicular to main axis of teeth), most external cusps much reduced.

Remarks: *Cerithiopsis eiseni*, originally described from western Panama, is identical in teleoconch morphology to shells herein studied from Chile. The thick sculpture and ovate outline of the small shell, its dark brown color, a moderately slow development of the adapical spiral cord of teleoconch, the shape of the aperture and of the



Figures 1–9. *Cerithiopsis cisni* Strong and Hertlein, 1939. 1–9, MNRJ 23163. 1, 4, 3.0 mm long, 2, 3.1 mm long, 3, 3.4 mm long. 5–9, Same shell as 4. 5, Development of the adapical spiral cord of teleoconch. 6–7, Body whorl, frontal and dorsal view. 8–9, Protoconch, frontal and apical view. Scale bars: 1–4 = 1 mm; 5–7 = 500 µm; 8–9 = 100 µm.



Figures 10–18. *Cerithiopsis eiseni* Strong and Hertlein, 1939. **10–18.** MNRJ 23163. **10–14.** External morphology of soft parts; 10–12, same individual, 13–14, another. **15.** Operculum. **16–18.** Marginal radular teeth. Scale bars: 10–14 = 500 µm; 15 = 100 µm; 16, 18 = 5 µm; 17 = 10 µm.

basal cords are the main features shared by them, in addition to an apparent bathymetric restriction to the shore zone. However, the type material of *C. eiseni* does not have a protoconch, precluding further comparisons

in relation to this structure. The original record of *C. eiseni* from Galapagos by Hertlein and Strong (1955) requires confirmation, because no shell was figured and cerithiopsids may have a restricted larval dispersal in

the open sea when compared to triphorids (Fernandes and Pimenta, 2017b).

Cerithiopsis eiseni shares some features with the Panamic species *Cerithiopsis neglecta* (C.B. Adams, 1852), including the brownish shell and similar teleoconch sculpture, but *C. eiseni* can be distinguished by the larger nodules on teleoconch, more ovoid shell shape, and light-colored protoconch with less whorls and weaker ornamentation. The Californian species *Cerithiopsis oxyx* Bartsch, 1911 also has a similar protoconch/teleoconch sculpture, but has a more elongated and lighter-colored shell, with the adapical cord of teleoconch strengthening much earlier than in *C. eiseni*.

The operculum of *C. eiseni* follows the 'pattern 2' described by Marshall (1978), possessing a submarginal or eccentric nucleus, which is found in several genera but not *Cerithiopsis* sensu Marshall (1978)—which causes a problem with that generic definition (Cecalupo and Robba, 2010; Modica et al., 2013). The ovate shell outline and presence of thick basal cords in *C. eiseni* (Figure 6) are more similar to *Joculator* Hedley, 1909 than to *Cerithiopsis*. These two genera certainly share considerable conchological intersections especially after recent works (e.g., Jay and Drivas, 2002; Cecalupo and Perugia, 2012, 2013, 2014) that substantially increased the amount of known *Joculator* species, and both may be proved to contain a number of non-natural groups after a robust phylogenetic approach. Similar opercula to *C. eiseni* include those of *Joculator* cf. *varians* Laseron, 1956 (Nützel, 1998: fig. 6D), one species of the complex of *Cerithiopsis tubercularis* (Montagu, 1803) (Nützel, 1998: fig. 1E) and *Tubercliopsis macalpinei* (Laseron, 1951) (Laseron, 1951: fig. 40), in addition to some species of the newtoniellid genus *Retilaskeya* (e.g., Marshall, 1978: fig. 3L).

The marginal teeth of *C. eiseni* fit the concept of the "spaghetti-radula" or "Cerithiopsis-group" radula defined by Nützel (1998), comprising several species (including some of *Cerithiopsis*) that bear elongated teeth. We include the radula of the western Atlantic species *Cerithiopsis prieguei* Rolán and Espinosa, 1996, *Cerithiopsis aimen* Rolán and Espinosa, 1996 and *Cerithiopsis gemmulosa* (C. B. Adams, 1850)—illustrated in Rolán and Espinosa (1996) and Rolán et al. (2007)—in the list presented by Nützel (1998). In contrast, the "Synthopsis-group" radula defined by Nützel (1998) bears brush-like teeth, with short and broad basal plates and numerous thin cusps. As addressed by Nützel (1998), the "Synthopsis-group" includes the genus *Joculator*, and it is clearly different from the radula of *C. eiseni*. A phylogeny is necessary to elucidate the generic allocation of this species, which has the shell more similar to *Joculator*, whereas the radula fits the concept of Nützel's "Cerithiopsis-group".

Geographic Distribution: Panama: Honda Bay (type locality); Chile: Caldera (this study). The record from Galapagos requires further confirmation.

Bathymetric Distribution: shallow subtidal (this study) to 16 m (type locality).

Family Triphoridae Gray, 1847

Genus *Monophorus* Grillo, 1877

Type Species: *Trochus perversus* Linnaeus, 1758, by monotypy. Recent, northeastern Atlantic and Mediterranean.

Monophorus monocelha new species

(Figures 19–43)

Triphorinae sp.: Romero and Valdebenito (2002: 498, fig. 6).

Type Locality: 27°05'15" S, 70°51'29" W, Calderilla beach, under sunken rocks at very low tide, Caldera, Región de Atacama, Chile.

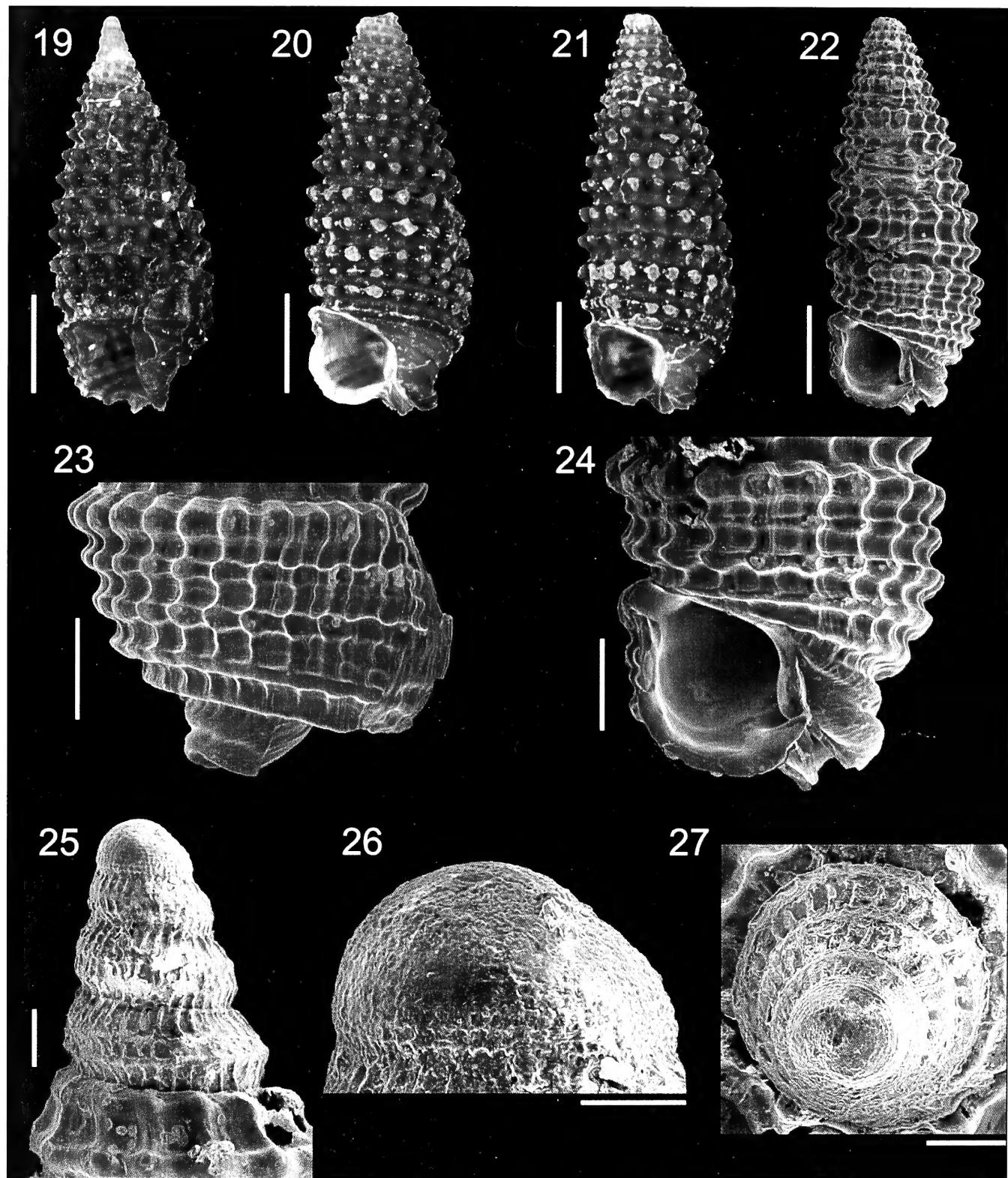
Type Material: Holotype: MNRJ 23164, J.F. Araya and M. Araya coll., 09/ii/2016. **Paratypes:** MNRJ 23165, type locality, J.F. Araya and M. Araya coll., 09/ii/2016, 7 specimens, 4 d.

Additional Material Examined: MZSP 118802, 26°57'17" S, 70°48'05" W, Los Patos Sector, Caldera, Región de Atacama, J. F. Araya coll., October 10, 2012, 12 shells, worn; MZSP 118806, Calderilla Beach, in sand at low tide, Caldera, Región de Atacama, J. F. Araya and M. Araya coll., August 12, 2012, 3 shells, worn.

Etymology: the specific name alludes to the brown mark between the eyes of specimens, resembling a unibrow (in Portuguese, "monocelha"). Epithet as a noun in apposition.

Diagnosis: very thick shell, brown teleoconch, yellowish protoconch; median spiral cord emerges between sixth/seventh whorl; brown mark between the eyes; radula 4-1-1-4.

Description: Shell: Sinistral, elongated, very thick, cyrtoconoid, slightly concave profile, up to 4.7 mm long (broken apex), 1.8 mm wide, ratio length/width 2.4 to 2.5. Protoconch multispiral, conical/cylindrical, 0.45–0.48 mm long, 0.36–0.40 mm wide; 4.5 convex whorls, well-defined transition between protoconch and teleoconch; embryonic shell dome-shaped, reticulate sculpture; larval shell with two distinct spiral cords, situated at 40% and 67% of last whorl height, entirely crossed by nearly orthocline axial ribs, numbering 32 in last whorl. Teleoconch with up to eight whorls; two main spiral cords at beginning, abapical one continuous to one on protoconch; median spiral cord emerges very weakly on sixth or seventh whorl, closely bordering adapical cord, gradually developing and reaching same size of abapical cord (adapical one more prominent on late whorls, 1.3× thicker than others at body whorl) after about one whorl; at body whorl, mean width of cords is equal or up to 1.4× higher than mean distance between cords; 19 to 21 orthocline axial ribs on seventh whorl; rounded nodules of large size; distinct and well-developed suture, with very small sutural cord; nodulose subperipheral cord, two equally thick basal cords, adapical one slightly to moderately nodulose, abapical one smooth; two small supranumerical cords may appear, one between median and abapical cords, another



Figures 19–27. *Monophorus monocelpha* new species. **19.** MNRJ 23164, holotype, 4.1 mm long. **20–22.** MNRJ 23165, paratypes, 4.1 mm long. **20–22.** 4.4 mm long. **23–24.** Body whorl, dorsal and frontal view, same shell as 22. **25–27.** Holotype. **25, 27.** Protoconch, frontal and apical view. **26.** Embryonic shell. Scale bars: 19–22 = 1 mm; 23–24 = 500 µm; 25, 27 = 100 µm; 26 = 50 µm.

between abapical and subperipheral cords; small and oval aperture, 0.84–0.95 mm long, 0.73–0.75 mm wide, ratio length/width 1.2 to 1.3; anterior canal curved downward/backward, open or partly closed by projection of outer lip, 0.40–0.43 mm long, 0.20–0.33 mm wide, ratio length/width 1.2 to 2.1; posterior canal as deep sinus, 0.18–0.23 mm long. Teleoconch brown to dark brown, protoconch yellowish.

External Morphology of Soft Parts: Color cream-white, with a brown and irregular stripe in the base of cephalic tentacles and between eyes, resembling a ‘uni-brow’; some black fecal pellets present along intestine, with a vesicular shape, anteriorly rounded and posteriorly acute, 87–115 µm long.

Operculum: Rounded/ovate, thin, semi-transparent, membranous, multisprial, poorly distinct whorls, nucleus sub-central, dislocated 15% to 22% from center toward margin; diameter of operculum exceeds diameter of opercular disc by 15% to 30%.

Jaw: With micro-pores on external side.

Radula: Formula 4-1-1-1-4; central, lateral and inner marginal teeth (M1 and M2) claw-shaped, outer marginal teeth (M3 and M4) somewhat hand-shaped; central tooth with five cusps, of which three central ones (cusps 2, 3, and 4) are triangular and wide (cusp 3 is 1.2–2× shorter than cusps 2 and 4), in addition to pair of small marginal cusps (cusps 1 and 5) that attain maximum length of 35% to 50% of cusps 2 and 4; lateral teeth with five (or six) triangular cusps of similar size, cusp 4 (or 5) can be up to 1.7× longer than remaining cusps, all cusps of lateral teeth narrower than three central cusps (2, 3, and 4) of central tooth; M1 usually with four cusps, cusp 3 more prominent (up to 1.3× longer than cusps 2 and 4), cusp 1 absent or up to 1.3× shorter than cusps 2 and 4; M2 with five to six cusps, external ones (cusps 1 and 5 or 6) reduced; M3 with four cusps, cusps 2 and 3 1.8–2.3× longer than cusps 1 and 4; M4 with four (or even five) cusps, external ones (cusps 1 and 4 or 5) reduced; central tooth 3.9–4.8 µm wide, lateral teeth 3.7–4.3 µm wide, M1 2.4–2.9 µm wide, M2 2.7–3.0 µm wide, M3 2.0–2.7 µm wide, M4 1.5–2.4 µm wide.

Remarks: Despite the great variation in shell color in the genus, many species of *Monophorus* have brown shells (e.g., Bouchet, 1985; Rolán and Peñas, 2001); this is the case of *Monophorus monocelha* new species. The new species is distinct from any other described triphorid from the eastern Pacific, showing some superficial similarity with the dark shells of *Triphora inconspicua* C. B. Adams, 1852, from western Panama, and *Triphora peninsularis* Bartsch, 1907, from Baja California. *Monophorus monocelha* differs from the holotype of *T. peninsularis* (USNM 106424) by having a much more developed suture, darker brown color (not pale brown as the holotype of *T. peninsularis*) and later emergence of the median spiral cord of teleoconch (in the sixth/seventh whorl of *M. monocelha*, but fourth whorl in the holotype of

T. peninsularis (M.R. Fernandes, pers. obs.) or fifth whorl (Bartsch, 1907). One worn paratype of *T. peninsularis* (USNM 635558) more closely resembles *M. monocelha*, although still showing a much reduced suture; types of *T. peninsularis* will be illustrated in an oncoming study about Triphoroidea from the eastern Pacific (Fernandes et al., in prep.).

Monophorus monocelha corresponds to the larval form designated as “Triphorinae” in Romero and Valdebenito (2002: 498, fig. 6), from Punta de Lobos, ~330 km southern of the type locality. Sculpture, number of whorls, and length of protoconch (up to 0.48 mm in shells herein studied vs. 0.51 mm in Punta de Lobos) are nearly identical between them.

Monophorus monocelha has an unusual brown mark between the eyes (Figures 28, 30, 32), a feature also described (but not illustrated) for the eastern Atlantic species *Monophorus pantherinus* Rolán and Peñas, 2001, although *M. monocelha* does not have reddish patches along the head-foot as observed in most species of the genus (e.g., Bouchet and Guillemot, 1978; Bouchet, 1985); this, however, could be explained by discoloration caused by storage in ethanol. The simple morphology of the operculum (Figures 34–36) is similar to those described for the genus (e.g., Marshall, 1983; Fernandes and Rolán, 1988; Romani, 2015). The distinctive radula of *M. monocelha* shows only four marginal teeth in each side (Figure 40), the smallest number of teeth per row so far recorded in *Monophorus*. The previous smallest numbers of teeth per row were those of *Monophorus ateralbus* Rolán and Fernández-Garcés, 1994 and *M. pantherinus*, both with six marginal teeth on each side.

Geographic Distribution: Chile: Caldera.

Bathymetric Distribution: shallow subtidal.

Genus *Inella* Bayle, 1879

Type Species: *Triforis (Ino) gigas* Hinds, 1843, subsequent designation by Jousseaume (1884). Recent, southwestern Pacific.

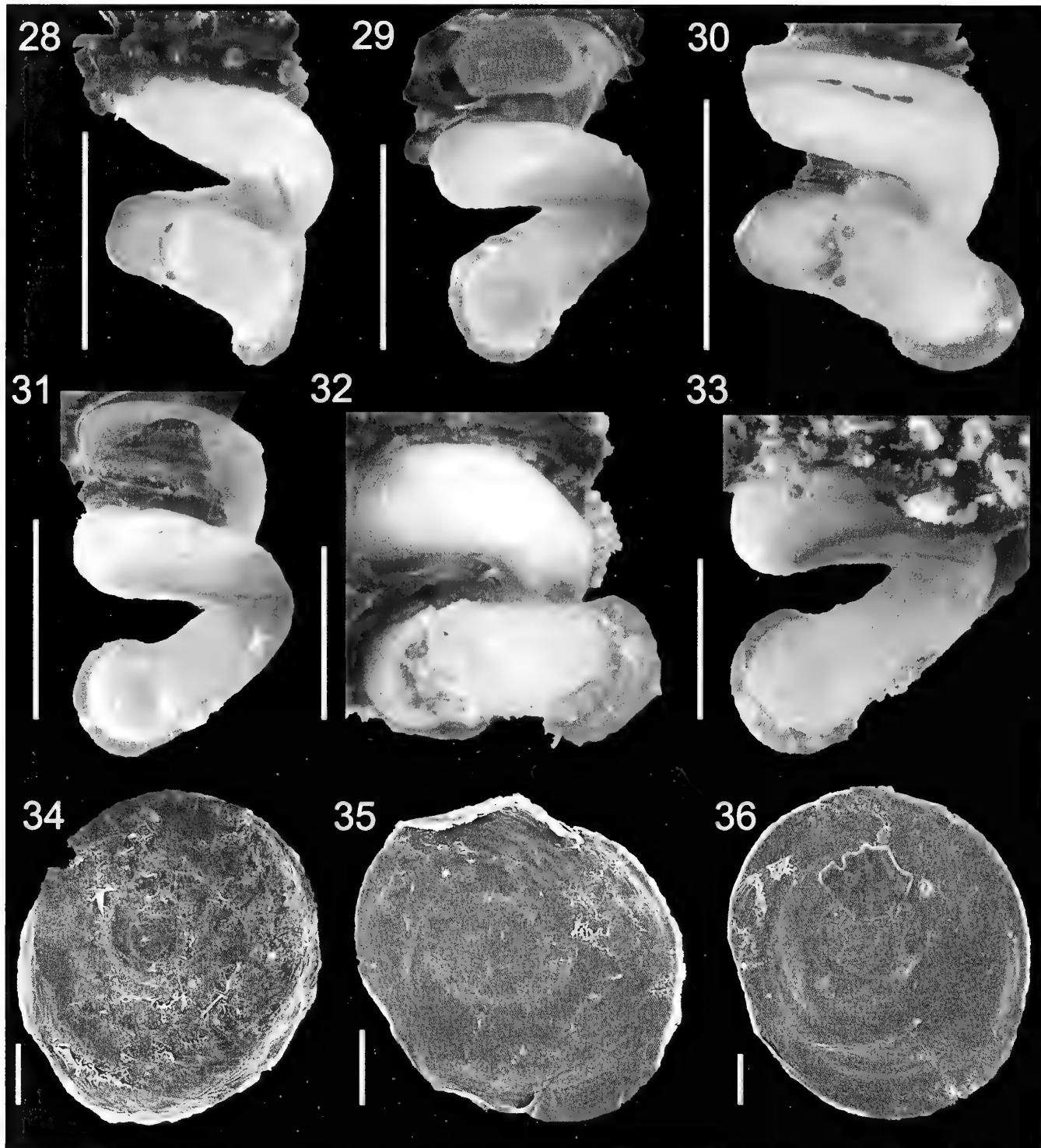
Inella basalis (Odhner, 1922) new combination (Figures 44–62)

Trifora basalis Odhner, 1922: 223, pl. 8, fig. 7; Rozbaczylo and Castilla (1987: 176, species list); Sandberg and Warén (1993: 122, species list).

Type Locality: Masatierra, 20–35 m, Juan Fernandez Archipelago.

Type Material: The single shell described by Odhner was not found at the Gothenburg Natural History Museum (Dr. Kennet Lundin, pers. comm.), where other types of Odhner are stored, nor at the Swedish Museum of Natural History (Dr. Anna Persson, pers. comm.).

Material Examined: Robinson Crusoe Island, Juan Fernandez Archipelago: MNRJ 23161 [6 shells], MNRJ 23162, 4 shells, Cumberland Bay, among coarse sand and

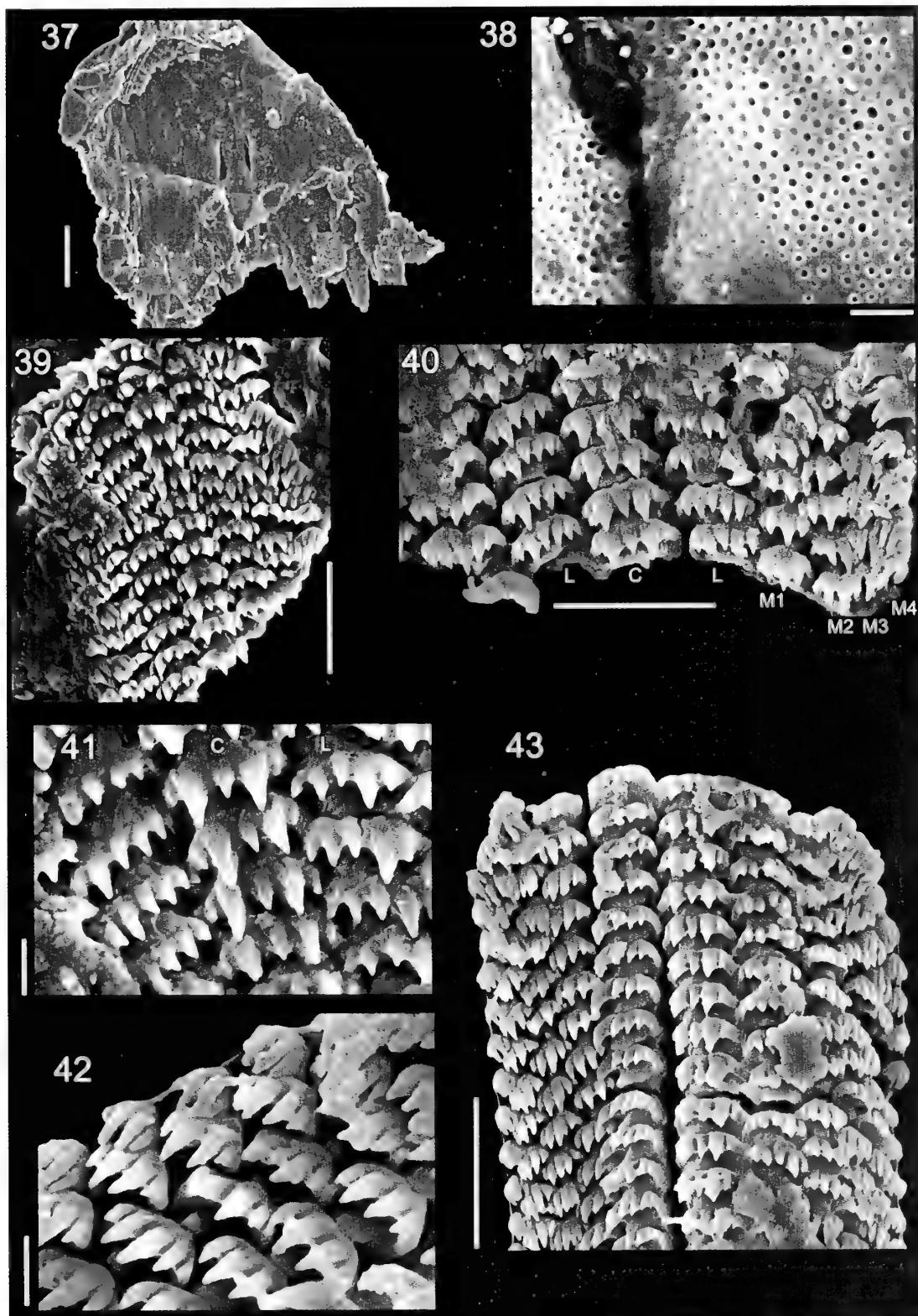


Figures 28–36. *Monophorus monocella* new species. 28–36. MNRJ 23165, paratypes. 28–33. External morphology of soft parts: 28–29, same individual; 30–31, other; 32–33, another. 34–36. Opercula. Scale bars: 28–31 = 1 mm; 32–33 = 500 μ m; 34–36 = 100 μ m.

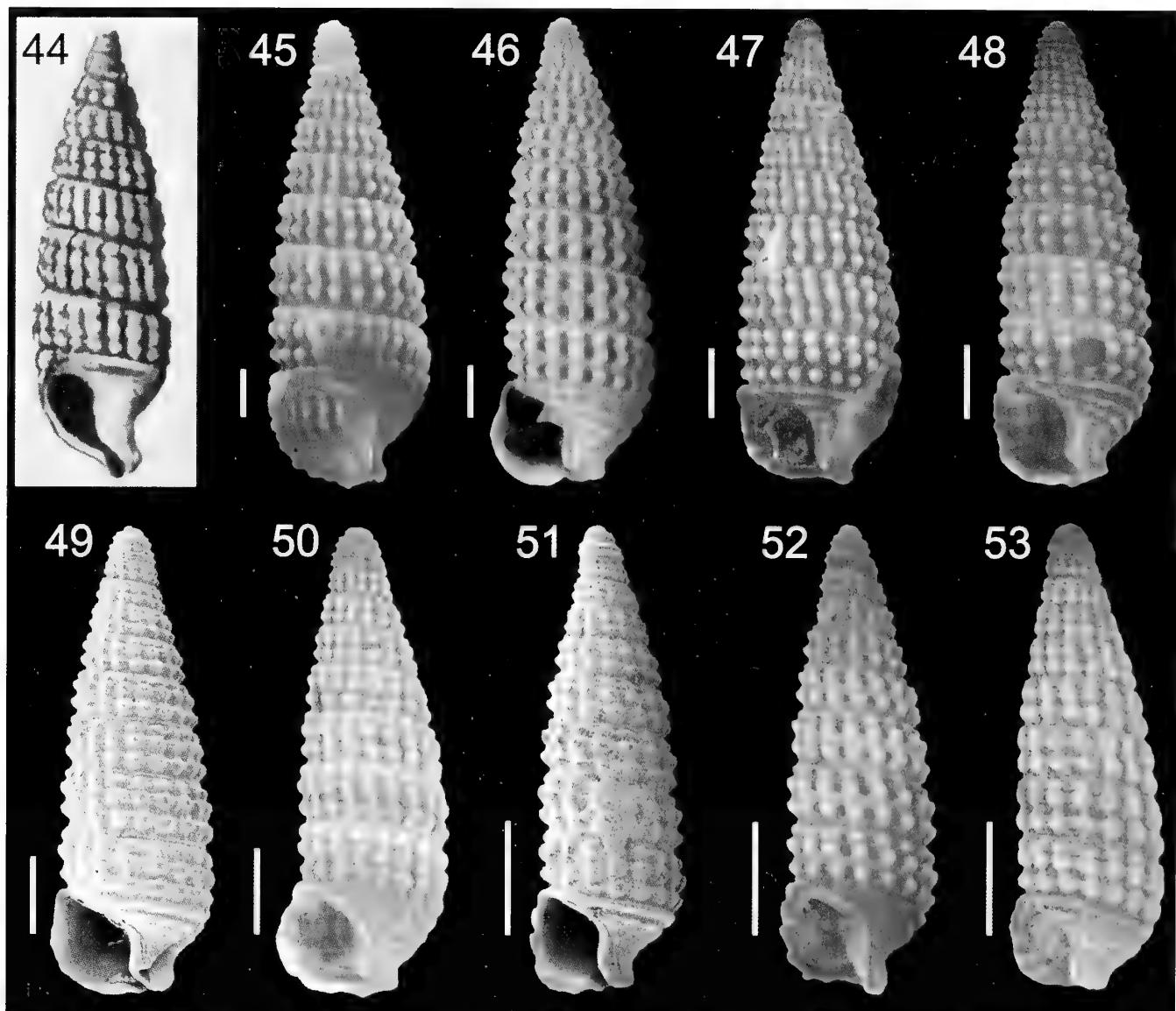
pebbles, February 2004; SBMNH 457461, 33°40'13" S, 78°56'11" W, El Padre Bay, March 25, 2004. 5 shells.

Description: Shell: Sinistral, elongated, cyrtoconoid, slightly concave profile, up to 9.9 mm long, 3.4 mm wide,

ratio length/width 2.9 to 3.2. Protoconch paucispiral, very short, blunt, 0.38–0.43 mm long, last whorl 0.45–0.66 mm wide; 2.0–2.5 somewhat axially compressed whorls, well-defined but gradual transition between protoconch (without nodules) and teleoconch (with nodules); first



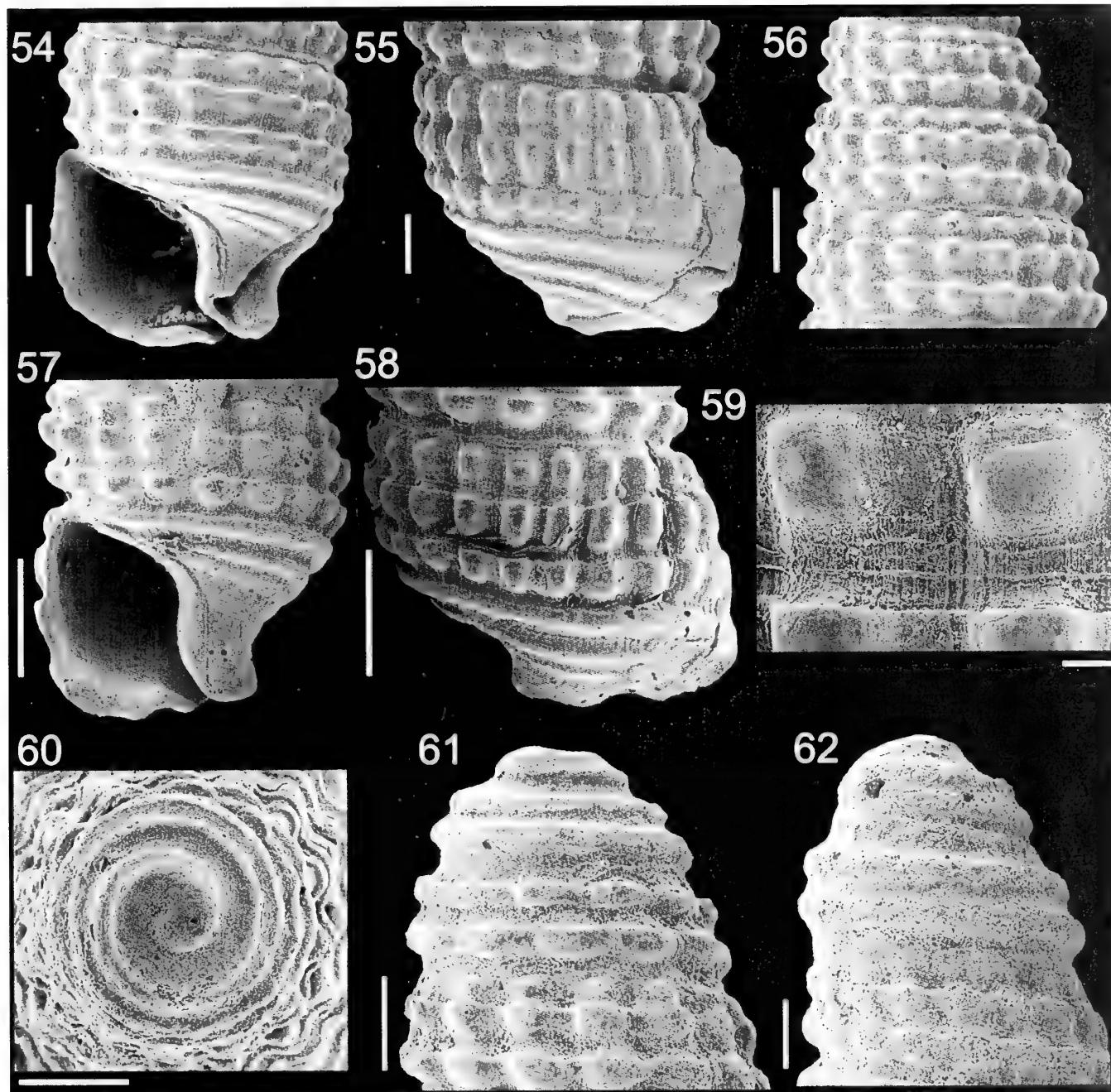
Figures 37–43. *Monophorus monocelha* new species 37–43. MNRJ 23165, paratypes. 37–38. Jaw, outer side. 39–43. Radula. Scale bars: 37 = 20 µm; 38 = 1 µm; 39–40, 43 = 10 µm; 41, 42 = 2 µm. Letters: C, central tooth; L, lateral teeth; M1–M4, marginal teeth.



Figures 44–53. *Inella basalis* (Odhner, 1922) new combination. **44.** Drawing of the holotype, from Odhner (1922: pl. 8, fig. 7). **45–46.** SBMNH 457461. **45.** 9.9 mm long. **46.** 9.1 mm long. **47–50.** MNRJ 23161. **47.** 6.8 mm long. **48.** 6.5 mm long. **49.** 6.4 mm long. **50.** 6.0 mm long. **51–53.** MNRJ 23162. **51.** 4.3 mm long. **52–53.** 4.1 mm long. Scale bars: 1 mm.

whorl small, depressed or slightly elevated; two strong, smooth spiral cords, situated at 22–39% and 62–76% of last whorl height, with nearly same size or abapical cord slightly more prominent toward end of protoconch; axial sculpture absent except for occasional minute axial marks above adapical cord. Teleoconch with up to 9.5 whorls; two spiral cords at beginning, both continuous to equivalent cords on protoconch; adapical spiral cord appearing on first or second whorl, gradually developing and reaching nearly same size of other cords on sixth/eighth whorl; at body whorl, mean width of cords 1.2–1.8× higher than mean distance between cords; spiral microsculpture may occur between cords, especially on late whorls; 15 to 21 nearly orthocline (sometimes slightly opisthocline) axial ribs on seventh

whorl; rounded (especially adapical and median cords) to slightly elliptical (especially abapical cord) nodules of large size; well-developed suture, with distinct sutural cord; thick, smooth subperipheral cord, two to four smooth basal cords, equally spaced; two small supernumerical cords may appear, one between median and abapical cords, other between abapical and subperipheral cords; ovate aperture, 0.81–2.10 mm long, 0.52–1.44 mm wide, ratio length/width 1.3 to 1.6; anterior canal very short, moderately wide, entirely open, 0.20–0.47 mm long, 0.23–0.54 mm wide, ratio length/width 0.8 to 1.0; posterior canal as a moderately deep, triangular notch, 0.11–0.31 mm long. Shell cream, beige, rarely light brown, with light brown internodular spaces.



Figures 54–62. *Inella basalis* (Odhner, 1922) new combination. **54–56, 60–61.** MNRJ 23161. **57–59, 62.** MNRJ 23162. **54–55,** **57–58.** Body whorl, ventral and dorsal view. **56.** Development of the adapical spiral cord of teleoconch. **59.** Spiral microsculpture in the body whorl. **60–62.** Protoconch, apical and frontal view. Scale bars: 54–58 = 500 µm; 59 = 50 µm; 60–61 = 250 µm; 62 = 100 µm.

Remarks: Despite Odhner's (1922) statement that the type of *I. basalis* has a broken apex, the described features of the teleoconch agree with the material herein examined, including the presence of four basal cords (two to four cords in this study; Figures 54, 57), shell dimensions of 6.3×2.0 mm (up to 9.9×3.4 mm in this study) and adapical spiral teleoconch cord reaching same size of other cords since fifth whorl (but since sixth whorl or later in this study). *Inella basalis* shows considerable intraspecific variation in

some shell features, such as: adult size (3.5–9.9 mm); shape of protoconch (more or less axially compressed, blunt and wide); number of axial ribs in the teleoconch (seventh whorl: 15 to 21); number of basal cords (two to four); and presence of supranumerical cords.

We abstain from designating a neotype for *I. basalis* due to an ongoing search and attempts at retrieval of past-due loans from the Gothenburg Natural History Museum to other institutions. Such search may still yield the return of

the holotype to that institution (Dr. Kennet Lundin, pers. comm.).

Geographic Distribution: Chile: Juan Fernandez Archipelago (type locality).

Bathymetric Distribution: 20–35 m (type locality).

DISCUSSION

The present study records *Inella basalis* (Odhner, 1922) **new combination** in the Juan Fernandez Archipelago almost a century after its original description. Two species from the northern continental shelf of Chile are also studied, the cerithiopsid *Cerithiopsis eiseni* Strong and Hertlein, 1939, previously known with certainty only from western Panama, and the triphorid *Monophorus monocelha* **new species**. These are the only extant species of both families from the continental shelf of Chile, in addition to *Cerithiopsis magellanica*. The reduced richness of Triphoroidea therein might be explained by the low water temperatures of the Warm Temperate Southeastern Pacific province (Spalding et al., 2007) and/or merely reflects inadequate sampling. The taxonomy of eastern Pacific Triphoroidea has been never revised and is highly problematic, owing to several species described from worn material and without illustrations in old works. An extensive review of Triphoroidea types from the eastern Pacific is being conducted (Fernandes et al., in prep.), aiming to provide the backbone for future descriptions.

The two species from northern continental shelf of Chile, *C. eiseni* and *M. monocelha*, have a similar shell morphology regarding the brown color, thickness, and narrow aperture. Very thick shells (with strong sculpture) and narrow apertures probably reduce the predation by crabs (Zipser and Vermeij, 1978; Bertness and Cunningham, 1981), considering that the eastern Pacific often presents gastropod shells thick and with narrow apertures as suggestive of anti-predation mechanisms (Vermeij, 1974). The existence of thicker shells of parasitic or micropredator snails, such as those of Triphoroidea, suggests frequent switch of hosts or preys, as this may be advantageous to avoid predation when outside of the protective cover furnished by hosts/preys (Vermeij, 2015). In addition, particular hydrodynamic conditions cannot be ruled out as sources of selective pressures for differences in shell thickness (e.g., Sitnikova and Maximova, 2016).

ACKNOWLEDGMENTS

We are grateful to: Dr. Kennet Lundin, Gothenburg Natural History Museum, for his tireless search for the type of *Inella basalis*; Drs. Alexander Nützel, Bruce Marshall, Daniel Geiger, and Emilio Rolán, for making several important suggestions during the review of the manuscript; Dr. Anders Warén, who helped with some references; and Camila Messias, for operating the SEM at the Department of Invertebrates (MNRJ). CNPq

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New species and record of *Diplommatina* Benson, 1849 (Gastropoda: Diplommatinidae) from Java, Indonesia

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ABSTRACT

Diplommatina (sensu lato) *majapahit* new species from Java is described and illustrated. A redescription and a new record for *D.* (sensu lato) *halimunensis* Nurinsiyah et Hausdorf, 2017 is provided.

Additional Keywords: Taxonomy, morphology, endemism, Greater Sunda Islands

INTRODUCTION

The Diplommatinidae of Java were recently revised (Nurinsiyah and Hausdorf, 2017) with 23 species recorded. *Diplommatina* (sensu lato) Benson, 1849 is the most diverse diplommatinid genus in Java (17 species) (Nurinsiyah and Hausdorf, 2017) and neighbouring Bali (6 of 10 species) (Vermeulen and Whitten, 1998). Recent sampling from Java provided new data on one insufficiently known species as well as a new species, which is described here.

MATERIALS AND METHODS

Recently collected material was stored in 99% ethanol. Terminology of morphological terms generally follows Liew et al. (2014), with modifications by Greķe (2017). The author's explanatory comments are placed in square brackets. Specimens were examined under a Leica S6D stereoscopic microscope. Photographs were taken with a Canon EOS 77D SLR camera attached to that microscope. Multiple photographs were taken at different focal planes and reassembled using CombineZP ® software. Scanning electron microscope (SEM) images were taken using SEM provided by the Latvian University's Faculty of Biology. Shells were cleaned mechanically with a brush and with KOH solution, air dried, and placed onto conductive tape on aluminum stubs. Shells were imaged using a Hitachi TM-3000 (Hitachi High Technologies ®) SEM following methods as described by Geiger et al. (2007). Abbreviations of depository institutions: KGC: Collection Kristīne Greķe, Rīga, Latvia; ZMHB: Museum für Naturkunde, Leibniz-Institut für

Evolutions- und Biodiversitätsforschung [formerly Museum für Naturkunde der Humboldt-Universität], Berlin, Germany; NME: Naturkundemuseum Erfurt, Germany; NMNL: National Museum of Natural History “Naturalis”, Leiden, the Netherlands.

RESULTS

Diplommatinidae L. Pfeiffer, 1856

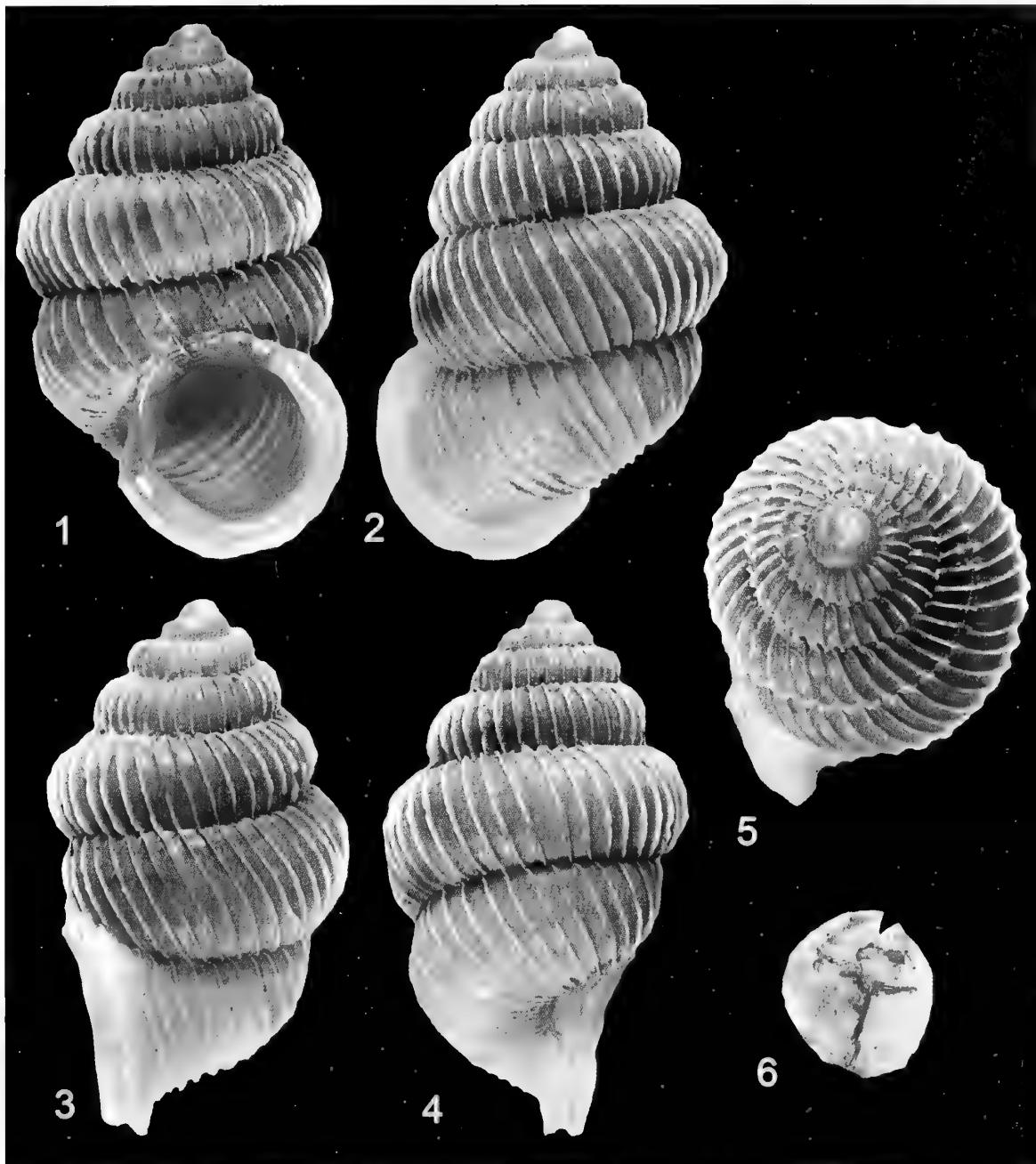
Diplommatina (sensu lato) Benson, 1849

***Diplommatina* (sensu lato) *majapahit* new species**
<http://zoobank.org/CF925B0C-7329-462B-B46E-CF9F96C7BDB>
(Figures 1–6, 23–27, 32–33)

Description: Shell large, pale yellowish to pale reddish, dextral, broadly conical with a convex apex. Holotype shell height (H) 4.5 mm, height of the ultimate whorl (HW) 2.6 mm, shell diameter (D) 2.5 mm, maximum diameter of peristome (PD) 2.1 mm. Adult paratypes:

Paratype No	H, mm	D, mm	PD, mm
1	4.8	2.7	2.1
2	4.7	2.8	2
3	4.6	2.4	2
4	4.5	2.5	1.9

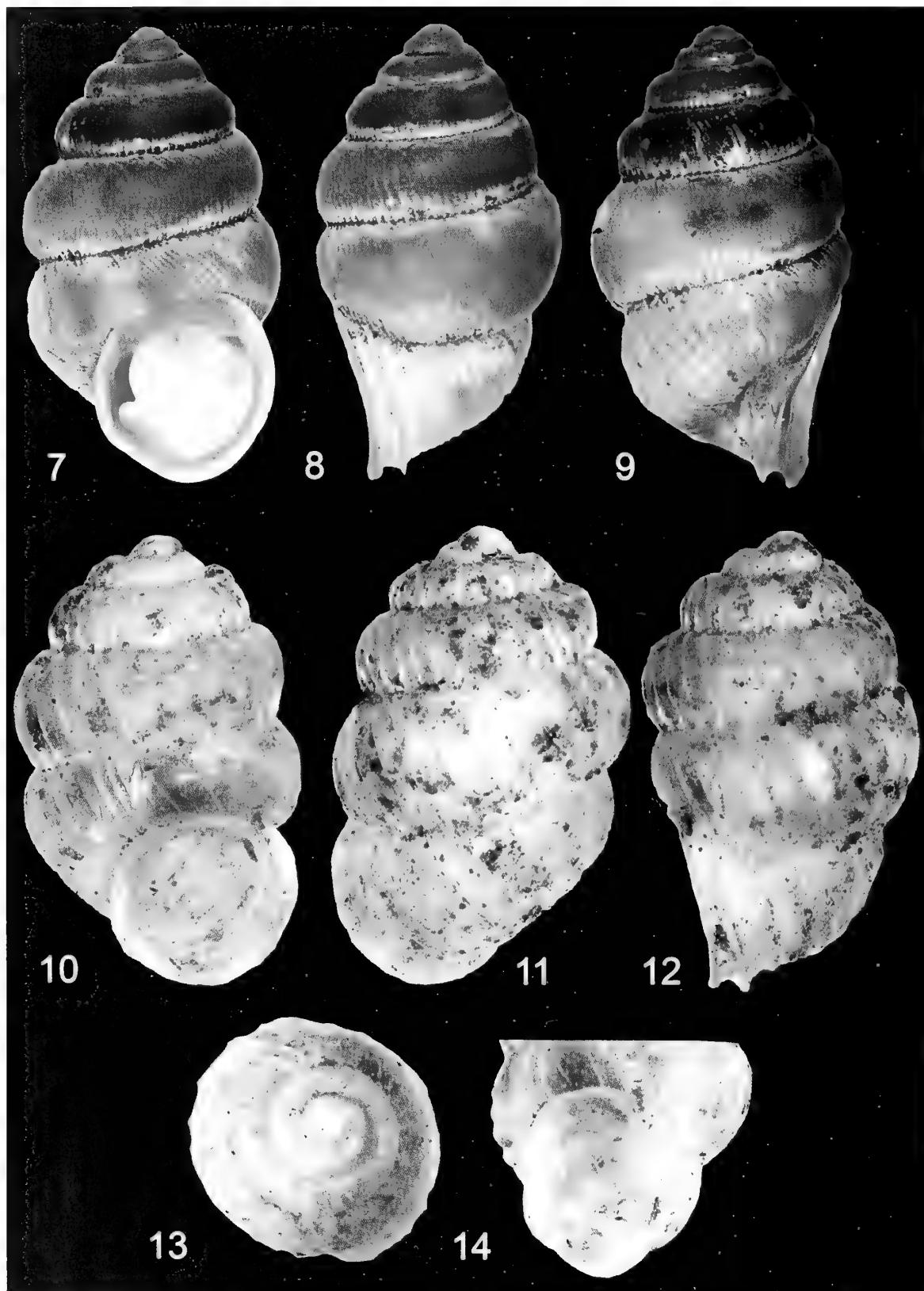
Shell with 6.5–7 convex whorls, the 1.5 embryonic whorl is microscopically pitted. The suture is rather deeply impressed. The ultimate whorl narrows in umbilical view (not visible in apical view), hardly wider than the penultimate whorl in apertural view. The umbilicus is closed in adults. The constriction is poorly defined, suture somewhat deeper at the constriction. The position of the constriction aligns with the parietal side of the aperture. The teleoconch is sculptured with coarse high and widely spaced axial ribs, which become slightly more widely spaced on the last half whorl. The ribs are generally straight. There are no abrupt changes in ribbing pattern. The ribs are not aligned with



Figures 1–6. *Diplomatina (sensu stricto) majapahit* new species, holotype: 1. Apertural view. 2. Abapertural view. 3, 4. Lateral view. 5. Apical view. 6. Operculum, outer surface.

those on previous whorls and are straight on earlier whorls, becoming slightly oblique to the coiling axis on the penultimate and the ultimate whorls. There are about 6 ribs per 1 mm on the penultimate whorl in apertural view. Spiral striations absent (Figure 32), delicate radial growth lines present on the ultimate whorl only (Figure 33). The aperture is slightly tilted in relation to the coiling axis (in lateral view; Figure 3), is circular, and has an entire apertural rim. The position of the aperture is more or less central against the coiling axis in apertural view. The peristome is double, obtuse angular at the transition from columellar to basal side. The outer peristome is broader than and expanding beyond

the inner peristome, broadly discontinued parietally. The inner peristome forms a continuous polished callus. The parietal margin of the peristome is attached to the ultimate whorl. The palatal and columellar margins of the outer peristome are slightly sinuous. There are two strong acute parietalis (Figures 26–27), one long and strong radial (vertical) palatalis (position of this lamella is almost central with regard to the parietal side of the peristome; Figure 1) and two long and strong longitudinal (horizontal) palatalis: the lower one \sim -shaped, somewhat shorter, level with columellar side of the peristome and upper one longer, straight situated somewhat beyond the columellar side of the peristome



Figures 7–14. *Diplomatina* (sensu stricto) *diplostoma* B. Rensch, 1931. **7–9.** Specimen from Mt. Adeng, Bali Island. **7.** Apertural view. **8, 9.** Lateral view. **10–14.** Holotype. **10.** Apertural view. **11.** Abapertural view. **12.** Lateral view. **13.** Apical view. **14.** Aperture, latero-ventral view.

(Figure 27). One strong obtuse columellar denticle (lamella) present, not directed downwards (Figure 1). The columella is broad, glossy, obliquely twisted and forming a very strong acute umbrella-like oblique columellar lamella in its lower third and with an indistinct knob just above the columellar lamella (Figures 23–25). The operculum is simple (primitive, of Greke 2017) - irregularly circular and translucent, paucispiral, without ridges (Figure 6).

Type Material: Holotype: NME unnumbered. **Paratypes:** Five specimens [3 adults and 1 juvenile KGC unnumbered, 1 adult NME unnumbered]. All August 20, 2017, leg. K. Greke, from type locality.

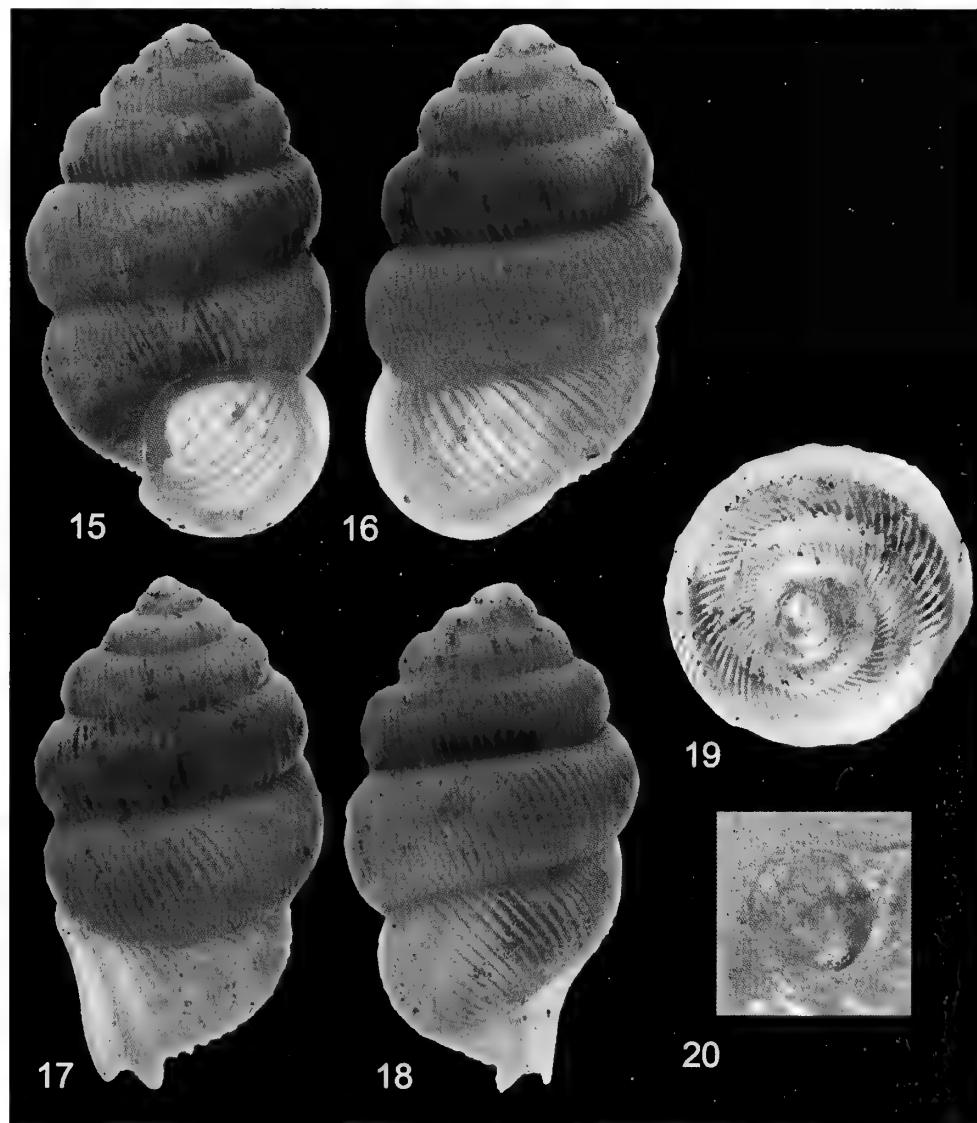
Type Locality: INDONESIA, E Java, ~46 km SE Malang, Tumpak Sewu waterfall, 8°12'54" S, 112°56'39" E, ~600–610 m, primary lowland rainforest vegetation on limestone cliffs, under large fallen leaves.

Ecology: Found in karst area of Tumpak Sewu waterfall. Specimens inhabit leaf litter accumulated in limestone cavities, observed at very wet place near the waterfall.

Etymology: The new species is named after the Majapahit Empire, a thalassocracy in Southeast Asia, based on the eastern part of Java (part of modern-day Indonesia), existed 1293–1500 and consisted of present-day Indonesia, Brunei, Malaysia, Singapore, Sulu Archipelago (the Philippines), southern Thailand, and East Timor. Named as a noun in apposition.

Distribution: Greater Sunda Islands: eastern part of Java (hitherto only known from type locality).

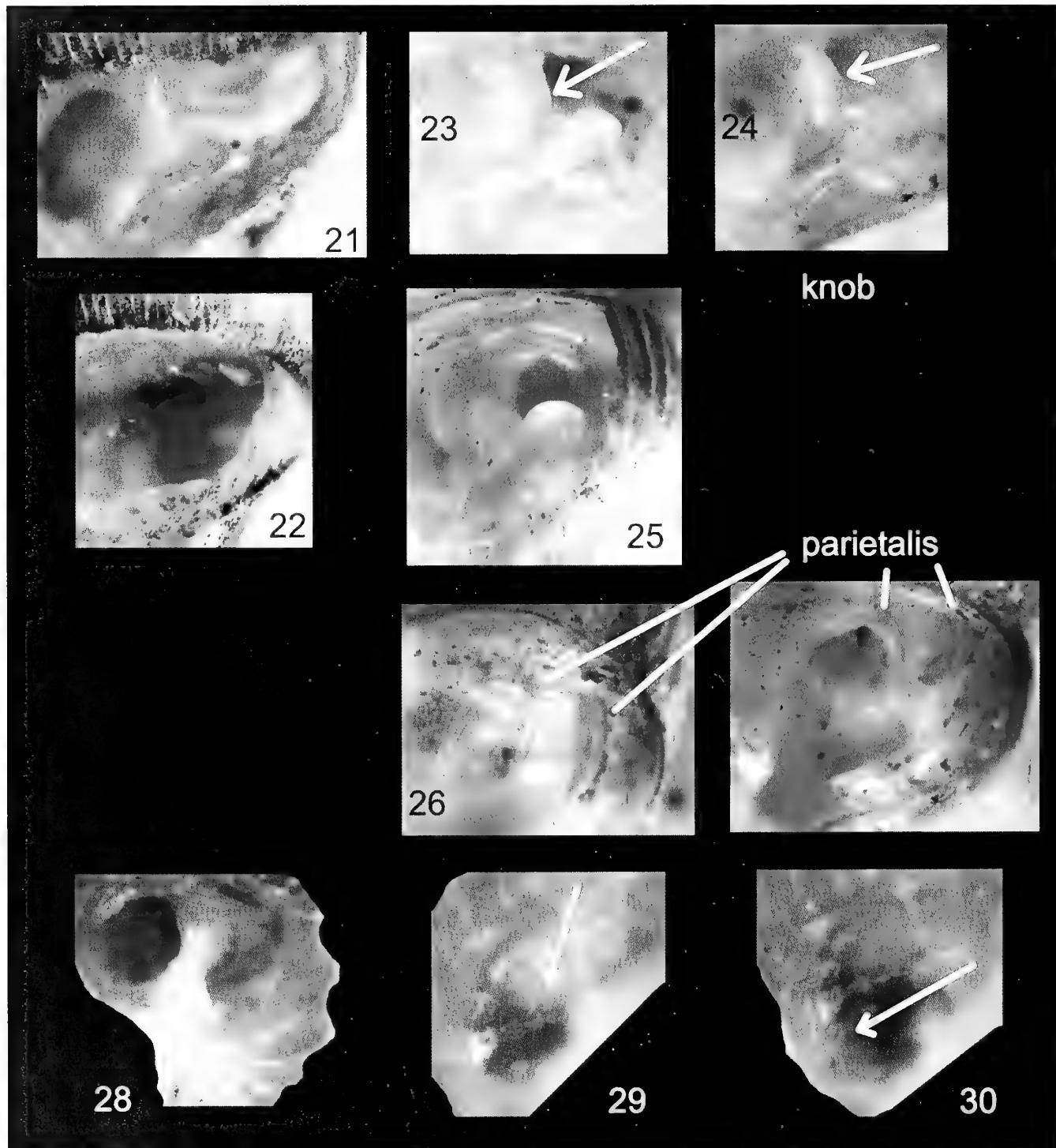
Differential Diagnosis: This is one of the largest Javan *Diplommatina* and is most similar to *D. (sensu lato) diplostoma* B. Rensch, 1931 sensu Vermeulen and Whitten



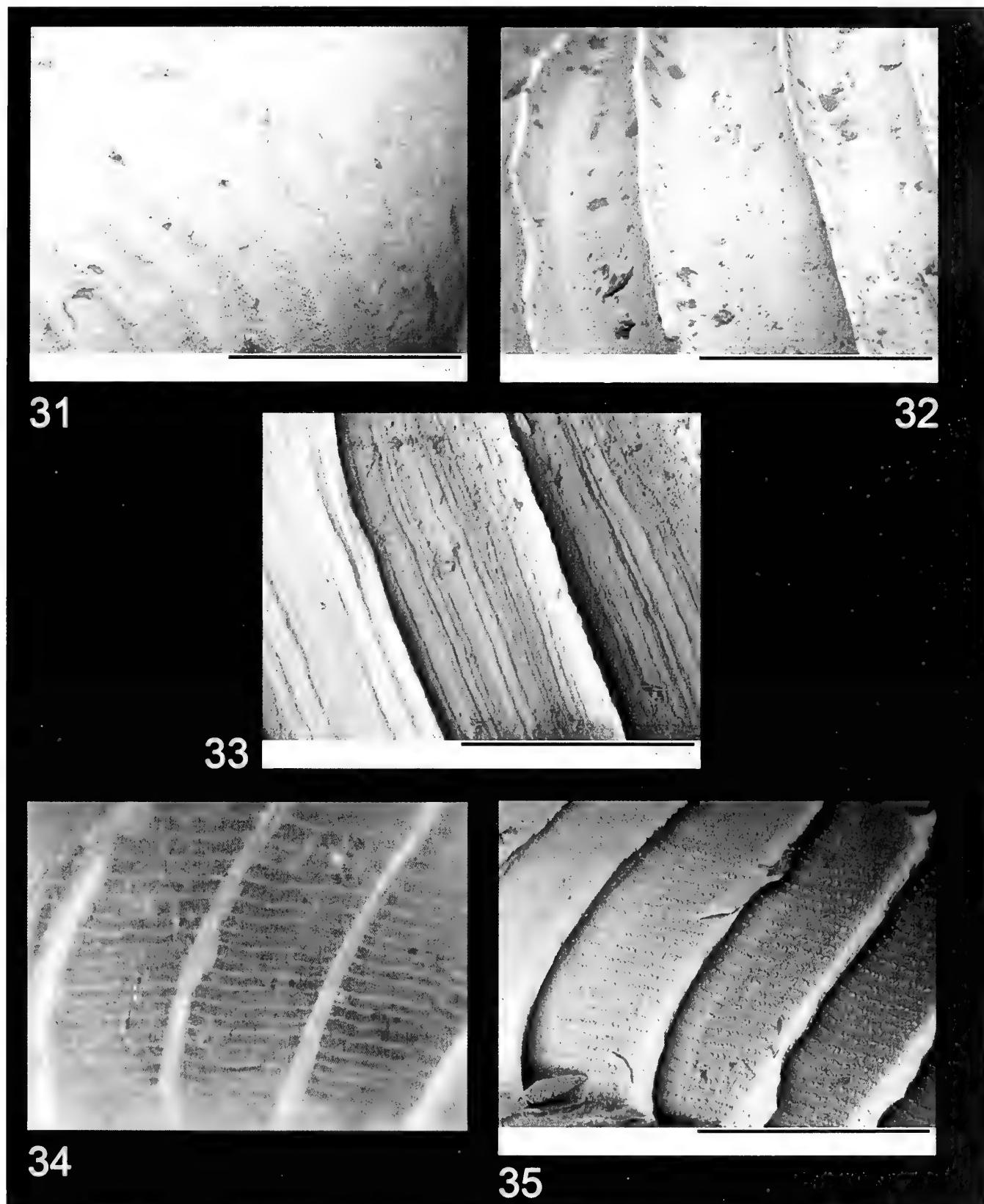
Figures 15–20. *Diplommatina* (sensu stricto) *duplicilabra* van Benthem Jutting, 1948 (*D. diplostoma* of authors), holotype. **15.** Apertural view. **16.** Abapertural view. **17, 18.** Lateral view. **19.** Apical view. **20.** Operculum, outer surface.

(1998), from Bali and Java. *Diplommatina diplostoma* is highly variable in shell shape and size, density of axial ribs. The following are significant features of *D. majapahit* new species: The inner peristome, weaker than the outer one,

forms a continuous broad polished callus in apertural view (the inner peristome is more prominent and does not form a polished callus in *D. diplostoma*); the columellar lamella is strong and thick (not acute as in *D. diplostoma*) and



Figures 21–30. Internal lamellae of the Javan and Balinese *Diplommatina* species. **21, 22.** *Diplommatina* (sensu stricto) *diplostoma* B. Rensch, 1931, specimen from Mt. Adeng, Bali Island. **21.** Columella and columnellar lamellae. **22.** Parietalis. **23–27.** *Diplommatina* (sensu stricto) *majapahit* new species, paratype. **23–25.** Columella (arrows indicate a knob) and columnellar lamella. **26.** Parietalis. **27.** All lamellae. **28–30.** *Diplommatina* (sensu stricto) *halimunensis* Nurinsiyah et Hausdorf, 2017, specimen from Mt. Salak, Java Island. **28.** Columella. **29.** Parietalis. **30.** Longitudinal palatalis. Not reproduced to the same scale.



Figures 31–35. Micrographs of the Javan and Balinese *Diplommatina* species. **31.** *D. (sensu stricto) diplostoma* B. Rensch, 1931, specimen from Mt. Adeng, Bali Island, penultimate whorl (visible numerous pores are result of shell degradation, not the actual microsculpture). **32–35.** *D. (sensu stricto) majapahit* new species paratype. **32.** Penultimate whorl. **33.** Last whorl (note delicate growth lines). **34, 35.** *D. (sensu stricto) halimunensis* Nurinsiyah et Hausdorf, 2017 specimen from Mt. Salak, Java Island, penultimate whorl.

provided with an indistinct knob above (columellar lamella acute, knob absent in *D. diplostoma*, including its type series). Palatal and parietal teeth are generally stronger in new species than in *D. diplostoma* (including types). The new species appears slightly larger (H 4.5–4.8 mm compared to 2.6–4.3 mm in *D. diplostoma*) and is one-half whorl bigger (6.5–7 whorls compared to 5.25–6.5 whorls in *D. diplostoma*, according to Nurinsiyah and Hausdorf (2017) and Greke (personal observations)).

Material Examined of *D. diplostoma*: Holotype [ZMHB] (Figures 7–14), Sunda=Expedition Rensch Fundort: [printed] Batoeriti (800m), Bali [handwritten] Datum: [printed] 3.-4.8.27 [handwritten] No: [printed] / Zoolog. Museum Berlin [printed] Diplommatina (Metadiancta ?) diplostoma Batoeriti Bali 800m 75427 Rensch leg [handwritten] / Zoolog. Museum Berlin [printed] Diplommatina (Metadiancta ?) diplostoma Rensch Zool. Jahrb. Syst., 61, p. 389, fig. 14, 1931 [handwritten] [label red]. Paratype [ZMHB], Sunda=Expedition Rensch Fundort: [printed] Batoeriti (800m), Bali [handwritten] Datum: [printed] 3.-4.8.27 [handwritten] No: [printed] / Zoolog. Museum Berlin [printed] Diplommatina (Metadiancta ?) diplostoma Rensch Paratypen. Batoeriti, Bali 75428 Rensch [handwritten]; additional material [8 adults KGC]: INDONESIA, Bali Is., Gunung Adeng mt., 08°19.402' S, 115°08.545' E, 1590 m, April 8, 2011, primary mid-montane rainforest, soil sample No 5, leg. A.Riedel.

Measurements *D. diplostoma*: Holotype H 3.5 mm, D 2.1 mm, HW 2 mm, PD 1.4 mm, 8–9 full ribs per 1 mm on the ultimate whorl in apertural view. Paratype *D. diplostoma*: H 3.8 mm, D 2.2 mm, HW 2 mm, PD 1.6 mm, 10 full ribs per 1 mm. Selected specimens from Bali: H 4.3 mm, D 2.5 mm, HW 2.3 mm, PD 1.9 mm; H 4.3 mm, D 2.4 mm, HW 2.3 mm, PD 1.7 mm; H 4.3 mm, D 2.4 mm, HW 2.3 mm, PD 1.8 mm.

Material Examined of *D. duplicilabra*: Holotype [NMNL] (Figures 15–20), Kawah Idjen. Merapi Wildreservaat 1600–1700 m 8.VIII.1931 C.Th.Cribb [handwritten] / type geteekend ex [handwritten] / type en paratypen [handwritten] Zoölog. Museum. Amsterdam. [printed] Diplommatina duplicilabra V.B.Jutting Kawah Idjen. Merapi Wildreservaat 1600–1700 m 8 Aug. 1931 leg.C.Th. Cribb [handwritten] STADTSDRUKKERIJ AMSTERDAM [printed] / holotype 3.48.005 1 dr ZOOLOGISCH MUSEUM AMSTERDAM ZMA Moll. 135940 Diplommatinidae 080.0 Diplommatina duplicilabra Van Benthem Jutting, 1948 INDOENSIA Java Kawah Idjen Merapi Game Reserve, 1600–1700 m 1931 08 08 sta. Leg.C.T. Cribb Ex. coll. Original publication: Vn Benthem Jutting, W.S.S., 1948. Systematic studies on the non-marine Mollusca of Indo-Australian Archipelago I. Families Hydrocenidae, Helicinidae, Cyclophoridae, Pupinidae ... [partly unreadable] Autoref: Van Benthem Jutting, 1948c: 597–599, fig. 54 Add.publ: Notes: Current Scientific Name: *Diplommatina duplicilabra* Van

Benthem Jutting, 1948 Det. Operculum is glued on a separate paper card with handwritten text "operc.".

Measurements *D. duplicilabra*: Holotype H 3 mm, D 1.7 mm, HW 1.6 mm, PD 1.2 mm, 15–16 full ribs per 1 mm on the ultimate whorl in apertural view. Spiral striations not indicated.

After careful examination of types and additional specimens of *D. diplostoma*, as well as the holotype of *D. duplicilabra* van Benthem Jutting, 1948, it seems unlikely that *D. duplicilabra* should be considered a junior synonym of *D. diplostoma* as stated by Vermeulen and Whitten (1998) and followed by Nurinsiyah and Hausdorf (2017).

***Diplommatina (sensu lato) halimunensis* Nurinsiyah et Hausdorf, 2017**
(Figures 28–30, 34–35)

Material Examined: INDONESIA, W Java, Halimun-Salak NP, Mt. Salak, N of Kawah Ratu crater, 6°42'12" S, 106°42'10" E, August 30, 2017, 1225 m, primary lower montane rainforest, leaf litter, leg. D.Telnov [10 adult specimens KGC and 5 NME].

Notes: I provide illustrations of the internal lamellae of this species for the first time. Parietal lamella is weakly developed as a flat hump (Figure 29). Palatal lamella as in Figure 30. Columella glossy and thick, widened basally (Figure 28). In all studied specimens, spiral striations are distinct and dense, clearly visible under 80 \times magnification (Figure 34). There are 3–4 rows of spiral striae per 50 μ m measured on the penultimate whorl above the constriction under 300 \times magnification (Figure 35).

This species was originally described from three specimens sampled at Mt. Halimun (Nurinsiyah and Hausdorf, 2017). New material comes from dense and very wet leaf litter of Mt. Salak volcano's primary rainforest, that is 19–20 km NNE from the type locality in same geographical and geological area.

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A Paleocene species of *Procardia* (Bivalvia: Anomalodesmata: Parilimyidae) from the Katsuhira Formation in Urahoro Town, eastern Hokkaido, Japan

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ABSTRACT

A new species of anomalodesmataan bivalve, *Procardia inouei*, is described from the Paleocene (upper Selanian to lowest Thanetian) Katsuhira Formation in eastern Hokkaido, Japan. The genus *Procardia* flourished during the late Jurassic to Cretaceous, and this new species is the first Paleocene record of *Procardia*. *Procardia* clearly survived the end-Cretaceous mass extinction, and includes the late Eocene to early Miocene species *P. dolicha* (Suter, 1917) from New Zealand. The Recent species of *Panacca* Dall, 1905 can be distinguished from *Procardia* easily, but possibly were evolutionarily derived from *Procardia*.

Additional Keywords: Paleocene, bivalve, *Procardia*, new species, *Panacca*

INTRODUCTION

The parilimyid genus *Procardia* Meek, 1871 is one of the characteristic Mesozoic anomalodesmataan bivalves. Fossils of this genus have been found from the Upper Jurassic in Spain, the Lower Cretaceous in England, the Cenomanian in the United States Western Interior Sea and the Maastrichtian in Germany, Poland, Ukraine and Russia (Woods, 1909; Cox and Newell in Cox et al., 1969; Runnegar, 1974; Jablonski and Raup, 1999; Olóriz et al., 2003). Only one younger species has been recorded, the early Eocene to early Miocene species *Procardia dolicha* (Suter, 1917), from the South Island of New Zealand (Beu and Maxwell, 1990, p. 132, pl. 9h, i). Beu and Maxwell (1990) considered this species to be a relict from the Mesozoic Era in New Zealand.

On the other hand, *Procardia* is very similar to *Panacca* Dall, 1905, which now lives in lower sublittoral to abyssal depths. Eight species of *Panacca* are known, from off West Africa, Meteor Seamounts, Massachusetts, Chile, Indonesia, southwestern Japan and Tasmania (Coan, 2000; Krylova, 2006; Sasaki and Okutani, 2007). They are

carnivores or scavengers, burrowing in soft mud, and do not prefer cold waters (Morton, 1981, 1982; Huber, 2010). Probably because of their ecology and their fragile shell, their occurrence is so scarce that *Panacca africana* (Locard, 1898), *P. chilensis* Coan, 2000, *P. montana* Krylova, 2006, and *P. trigona* Sasaki and Okutani, 2007 were each based on a single specimen. However, there is no fossil record of this genus. *Panacca* differs from *Procardia* mainly by lacking a lunule.

One articulated bivalve specimen of *Procardia* has been collected from the Paleocene Katsuhira Formation (late Selanian to earliest Thanetian; see Amano et al., 2018) in eastern Hokkaido by Mr. K. Inoue (Obihiro City). I describe this species as new and discuss the relationship between *Procardia* and *Panacca*.

MATERIALS AND METHODS

One articulated specimen of *Procardia inouei* new species was obtained from the dark gray mudstone of the Katsuhira Formation exposed along the Urahoro River, 30 m north of the mouth of the Kokatsuhirazawa River, Urahoro Town, eastern Hokkaido (Figure 1; 42°59'12" N, 143°37'35" E). The new species was associated with *Meganuculana allenii* Amano and Jenkins, 2017, *Thyasira?* sp., *Neverita majimai* Amano and Jenkins, 2018, *Kangilioptera inouei* Amano and Jenkins, 2014 and *Biplica paleocenica* Amano and Jenkins, 2018. As observed by Amano et al. (2018), it is estimated that the Katsuhira Formation was deposited at a depth of 200 to 500 m.

The holotype of the new species is catalogued in the University Museum of the University of Tokyo (UMUT). The associated fauna is stored at College of Science and Engineering, Kanazawa University.

SYSTEMATIC PALEONTOLOGY

Superfamily Pholadomyoidea King, 1844

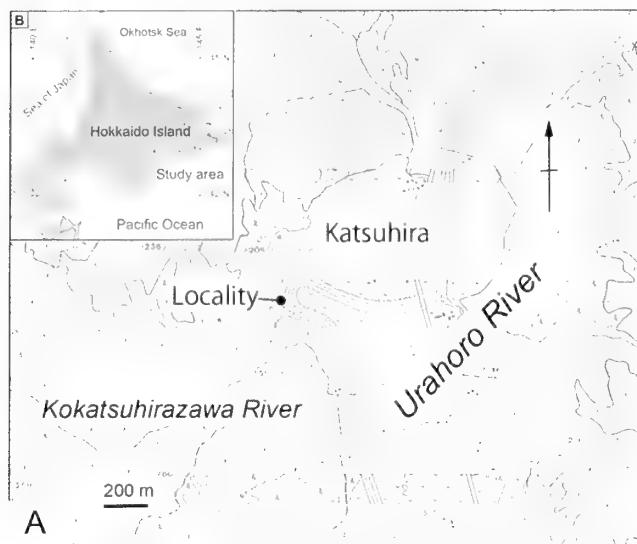


Figure 1. Map showing the type locality of *Procardia inouei* new species. Base map from “Katsuhira,” original scale 1:25,000; topographical map published by the Geospatial Information Authority of Japan.

Family Parilimyidae Morton, 1981

Remarks: This family was separated from Pholadomyidae King, 1844 based mainly on anatomical characters, by Morton (1981, 1982). Judging from the fossil record (Runnegar, 1974), Pholadomyoidea should be allocated on the basal part of the bivalve phylogenetic tree. Although the molecular sphylogeny of the Anomalodesmata has been examined by Dreyer et al. (2003) and Harper et al. (2006), Pholadomyoidea have not been included, probably because living specimens are difficult to obtain. Coan (2000), Krylova (2006), and Sasaki and Okutani (2007) mistakenly attributed the family Parilimyidae to Morton (1982). Morton (1981) had already proposed this family, as indicated by Huber (2010). When Coan (2000) included two genera, *Parilimya* Melvill and Standen, 1899 and *Panacca* Dall, 1905, he considered *Nipponopanacca* Habe, 1977 to be a synonym of *Parilimya*. However, as Matsukuma (1989) discussed, by comparing it with the type species of *Pholadomya*, *P. candida* G. B. Sowerby I, 1823, *Nipponopanacca* should be treated as a subgenus of *Pholadomya* G. B. Sowerby I, 1823 (see also Okutani, 2017). Runnegar (1974) suggested that *Panacca* is a junior synonym of the Mesozoic genus *Procardia* Meek, 1871. As discussed below, the genus *Panacca* is separated from *Procardia*, which is also included in Parilimyidae. Moreover, judging from its shape and shell sculpture, *Kanakimya* Campbell and Grant-Mackie, 1995, from Middle Jurassic rocks of New Caledonia, should be included in this family.

Genus *Procardia* Meek, 1871

Type Species: *Isocardia?* *hodgei* Meek, 1871 by original designation.

Remarks: *Procardia* is characterized by having an anteriorly truncated triangular shell, slightly higher than long or with height nearly equal to length, radial ribs present over the whole surface apart from the anterior flat area, some commarginal ribs or distinct growth lines, and a distinct lunule on the flat area. The Recent genus *Panacca* Dall, 1905 differs from *Procardia* by its longer shell and by having no radial ribs on the posterior end. Moreover, as pointed by Beu and Maxwell (1990), species of *Panacca* lack a lunule on the anterior flat area. *Kanakimya* was proposed by Campbell and Grant-Mackie (1995) as a subgenus of *Pholadomya* from Middle Jurassic rocks in New Caledonia, based on only one species, *Pholadomya (Kanakimya) uitoe* Campbell and Grant-Mackie, 1995. *Kanakimya* differs from *Procardia* by having a sub-truncated posterior margin and no radial ribs on the posterior surface, although it is similar to *Procardia* in having a high shell with an anterior flat area and a lunule.

Procardia inouei new species

(Figures 2–5)

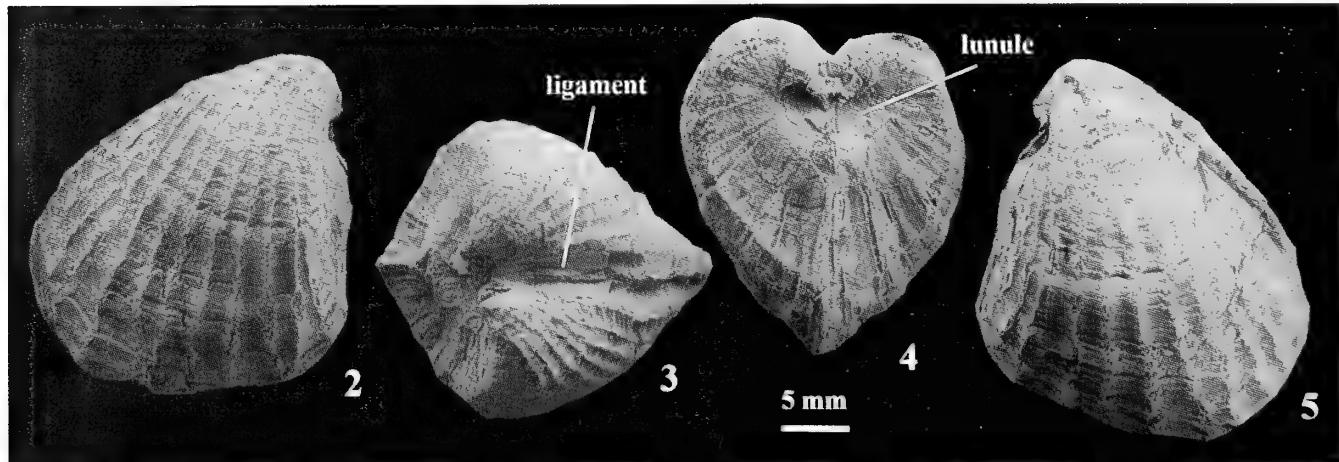
Diagnosis: Small, trigonal *Procardia* sculptured with 13 radial ribs. Radial ribs with central crest and gently sloping sides; interspaces each wider than one rib. Anterior flat area sculptured only with fine growth lines; with distinct lunule.

Description: Shell fragile, nacreous inside, small (24.9 mm in length), trigonal, slightly higher than long (height 25.2 mm), equivalve, extremely inequilateral. Posterior dorsal margin long, broadly arched, gradually merging into subcircular posterior margin; ventral margin nearly straight; anterior dorsal margin short; anterior margin slightly concave, truncated. Umbo well inflated, located at anterior one-eighth (12.4 %) of shell. Whole surface apart from anterior flat area sculptured with 13 radial ribs, each with central crest, gently sloping sides, and fine growth riblets; interspaces each wider than rib width. Anterior flat area sculptured with distinct fine growth lines. Lunule rather wide, moderately depressed, bounded by rough ridge. Escutcheon depressed, lanceolate, between strong radial ribs of both valves. Ligament external, occupying half of postero-dorsal margin. Interior characters unknown.

Type Material: Holotype: UMUT CM 33112 (length 24.9 mm; height, 25.2 mm; depth, 21.5 mm).

Type Locality: Cliff along Urahoro River, 30 m north of the mouth of Kokatsuhirazawa River, Urahoro Town, eastern Hokkaido, Japan.

Remarks: *Procardia inouei* new species is similar to *Procardia decussata* (Mantell, 1822) from the Cretaceous Chalk in southeastern England. Both have a triangular shell with radial ribs and growth riblets and a wide anterior flat area. However, the present new species is smaller (*P. decussata* attains 98 mm in length; Woods, 1909) and has fewer radial ribs than *P. decussata* (*P. decussata* has 18 radial ribs, which are fine on the posterior area).



Figures 2–5. *Procardia inouei* new species (holotype, UMUT CM 33112) from the Katsuhira Formation. **2.** Lateral view of right valve. **3.** Dorsal view. **4.** Anterior view. **5.** Lateral view of left valve.

Procardia hodgei (Meek, 1871), the type species of *Procardia*, from the Campanian Pierre Shale in the Interior Sea Way area in the USA, differs from the present new species by having many rounded radial ribs and distinct commarginal growth ribs (see Meek, 1876; Runnegar, 1974).

Marwick (1944) described *Cardium (Fragum) dolichum* Suter, 1917 and *C. (F.) maorinum* Suter, 1917, both with type specimens from the lower to middle Oligocene in the South Island of New Zealand, and referred both to *Procardia dolicha*. Beu and Maxwell (1990, p. 132, pl. 9h, i) illustrated this species and recorded it from late Eocene to early Miocene rocks in New Zealand. *Procardia dolicha* differs from *P. inouei* new species by having a larger shell (55 mm in length), more numerous radial ribs (25 to 28) and a narrower flat area with a more distinctly demarcated lunule.

Etymology: The new species is named for Kiyokazu Inoue (Obihiro City), the collector of the holotype.

Distribution: Known only from the type locality, in the upper Selanian to lowest Thanetian Katsuhira Formation, Urahoro Town, eastern Hokkaido.

DISCUSSION

This is the first record of *Procardia* in the Paleocene and from the northern Pacific region. As already mentioned by Beu and Maxwell (1990), this genus survived the end-Cretaceous mass extinction in New Zealand. Nine species or genera from the Katsuhira Formation were able to survive this event, partly because they lived in deep water (Amano et al., 2018). *Procardia inouei* new species is added to the relict forms from the Mesozoic fauna.

The oldest *Procardia* sp. is recorded from an Upper Jurassic carbonate with siliceous sponges in southern

Spain (Olóriz et al., 2003). In the Cretaceous, species of *Procardia* are widespread in Europe and US Interior Sea Way (Woods, 1909; Jablonski and Raup, 1999). However, there is no record of this genus from the Cretaceous in Japan (Nagao, 1943; Hayami, 1975; Tanaka and Toshimitsu, 2003). The migration route of this genus to Japan during the Paleocene is uncertain.

On the other hand, the present-day genus *Panacca* has a world-wide distribution in warm and relatively deep waters, but has no fossil record (Coan, 2000; Krylova, 2006; Sasaki and Okutani, 2007). The New Zealand relict species *Procardia dolicha* (Suter, 1917) is unusual in having a rather elongate shell similar to *Panacca*. However, the presence of radial ribs on whole surface and a lunule, which are characters of *Procardia*, were described and illustrated in *P. dolicha* by Marwick (1944) and Beu and Maxwell (1990). It is uncertain, but the elongate shape of *P. dolicha* suggests the possibility that *Panacca* evolved from *Procardia*.

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A large new *Wareniconcha* (Bivalvia: Vesicomyidae) from a Pliocene methane seep deposit in Leyte, Philippines

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ABSTRACT

A new species of the genus *Wareniconcha*, *W. mercenarioides*, belonging to the chemosymbiotic bivalve subfamily Pliocardiinae (family Vesicomyidae), is described from a Pliocene methane-seep deposit at Liog-Liog on Leyte Island, Philippines. With a length of almost 12 cm, this species is significantly larger than the six extant species currently considered as belonging to *Wareniconcha*. In addition to being very large, *W. mercenarioides* is more inflated and has a considerably more rounded shell outline compared to the oval shells of other *Wareniconcha* species. This is the first fossil record of *Wareniconcha*. Considering the overall similarity of the Leyte seep fauna to species living at vents and seeps in the vicinity of southern Japan, we anticipate that similarly large, and closely related species, might still be extant in the Indo-West Pacific region.

Additional Keywords: Indo-Pacific Ocean, hydrothermal vents, shell size, deep-sea

INTRODUCTION

Vesicomyid bivalves are a major component of faunal communities around many deep-sea hydrothermal vents, methane-seeps, and sunken whale carcasses (Boss and Turner, 1980; Paull et al., 1984; Smith et al., 1989; Kojima et al., 2004; Krylova and Sahling, 2010; Johnson et al., 2017). They thrive in these environments because they live in symbiosis with sulfur-oxidizing bacteria from which they obtain most, if not all, of their nutrients (Arp et al., 1984; Fisher, 1990). In addition to being abundant, several vesicomyid species reach very large sizes, such as '*Ectenagena*' *extenta* from methane-seeps in Monterey Canyon (up to 24.5 cm; Krylova and Moskalev, 1996), the iconic '*Calyptogena*' *magnifica* from vents on the East Pacific Rise and Galapagos Ridge that reaches 26.3 cm in length (Boss and Turner 1980), and *Abyssogena novacula* Krylova, Sahling, and Janssen, 2010 reaching 27.7 cm in length (Krylova et al. 2010).

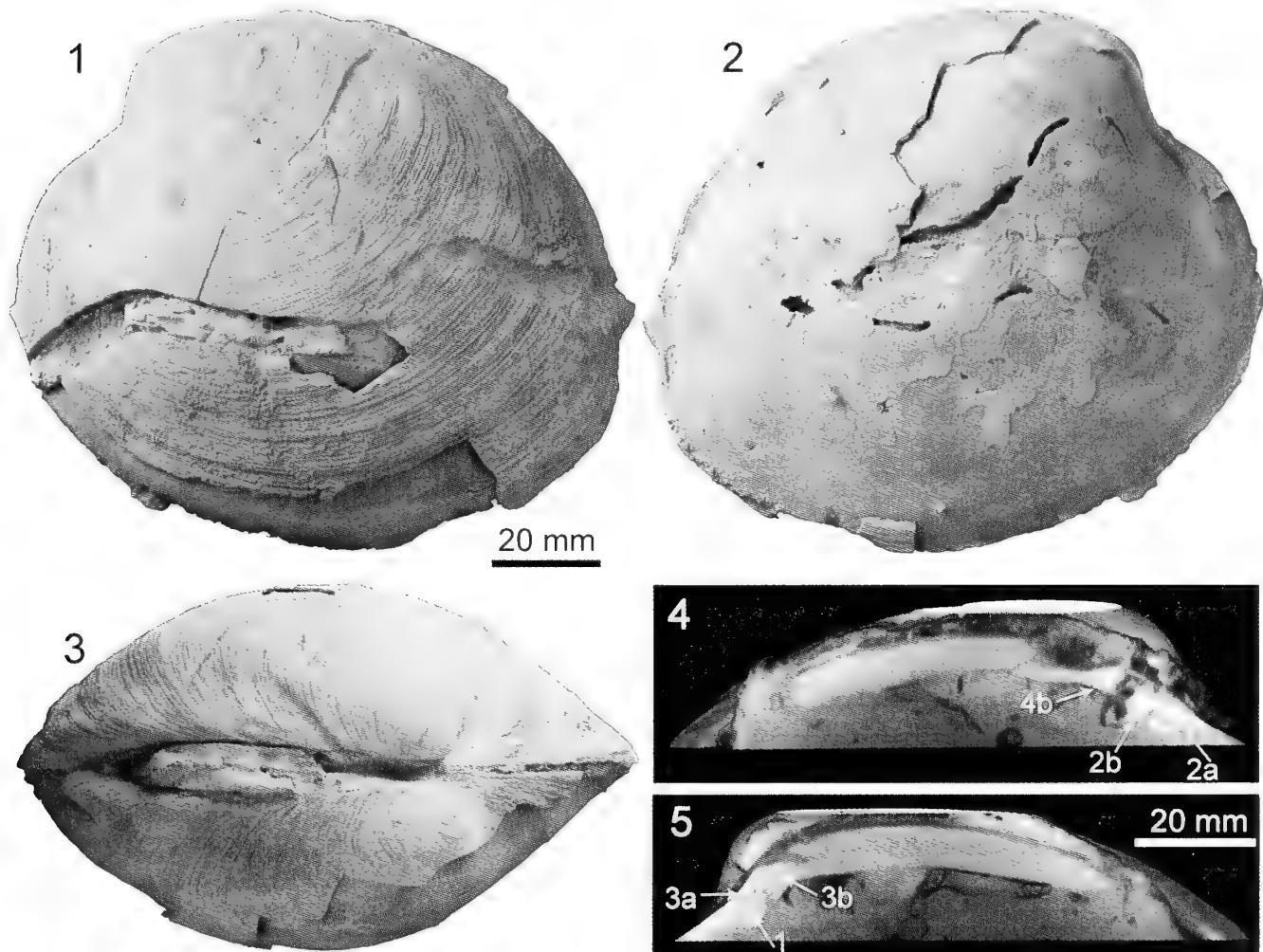
In comparison to these large species, members of the vesicomyid genus *Wareniconcha* reach only moderate

sizes of up to 7.6 cm, as in the case of the type species *Wareniconcha guineensis* (Thiele and Jaeckel, 1931) from methane seeps in the eastern Atlantic Ocean. Other species subsequently considered as belonging to *Wareniconcha* reach similar sizes (e.g., both *W. winckworthi* (Prashad, 1932) and *W. solidissima* (Prashad, 1932) from the Bali Sea in Indonesia reach about 7 cm), whereas others are somewhat smaller (e.g., *W. ovalis* (Dall 1895) from the eastern Pacific, and *W. cretacea* (Smith, 1906) from West of Sri Lanka in the Indian Ocean, reach 5–6 cm in length). Here we describe a new species of *Wareniconcha* from Pliocene seep deposits in Leyte Island, Philippines that reaches nearly 12 cm in length.

Chemosymbiotic bivalves of the mytilid subfamily Bathymodiolinae show a remarkable increase in size through geologic time that can be linked to the acquisition of different types of symbiotic associations (Lorion et al., 2013). In addition, vesicomyid bivalves showed an increase in shell size since their first appearance in the middle Eocene (Kanie and Kuramochi, 2001; Amano and Kiel, 2007, 2011; Amano et al., 2014). Although vesicomyid bivalves do not show the diversity of symbiotic associations as bathymodiolins do, vesicomyid clades show a diversity of sulfide-binding affinities that enable (or restrict) them to colonize distinct niches within methane seep sites related to sulfide flux and availability (Barry and Kochevar, 1998; Goffredi and Barry, 2002; Decker et al., 2014). Future studies of shell size and sulfide-binding affinities could provide new insights into the long-term evolution of these traits through Earth's history.

MATERIALS AND METHODS

Several methane-seep deposits have been discovered in deep-water strata of the Visayan back-arc basin along the northwestern coast of the island of Leyte in the Philippines (Majima et al., 2007; Majima et al., 2010). These massive mudstones were mapped as Bata Formation and initially considered late Miocene in age (Corby and al., 1951; Porth et al., 1989; Mines and Geosciences Bureau, 2010). The



Figures 1–5. *Wareniconcha mercenarioides* new species; holotype (NMNS PM 28168). **1.** Left valve. **2.** Right valve. **3.** Dorsal view. **4.** Hinge and ligament nymph of left valve, micro-CT scan. **5.** Hinge and ligament nymph of right valve, micro-CT scan.

specimens reported here were obtained from a giant calcareous concretion packed with chemosynthetic bivalves, found exposed at Liog-Liog Point between Tabango and Campopo bays, at 11°17'37.7" N, 124°21'57.5" E (Majima et al., 2007). Ongoing stratigraphic and micropaleontologic work indicates that the Bata Formation exposed around the Liog-Liog Point ranges in age from late Pliocene to early Pleistocene, and the giant concretion is likely to have been derived from the upper Pliocene part of the Bata Formation. The type material is deposited at the National Museum of Nature and Science, Tsukuba, Japan (NMNS PM 28168, PM 28169) and the National Museum, Manila, Philippines (NMP-2148).

To observe the hinge structure, we performed non-destructive analysis using an X-ray microfocus CT system (TESCO TXS320-ACTIS) at the National Museum of Nature and Science, Tokyo, at experimental conditions of 247 kV and 240 μ A. The resolution of the square slice CT was 97 mm per 1024 pixels, and the spacing between each CT slice was 0.1 mm. Analysis and surface rendering were

performed using the software OsiriX version 3.9.2 32-bit (an open-source DICOM viewer for Macintosh).

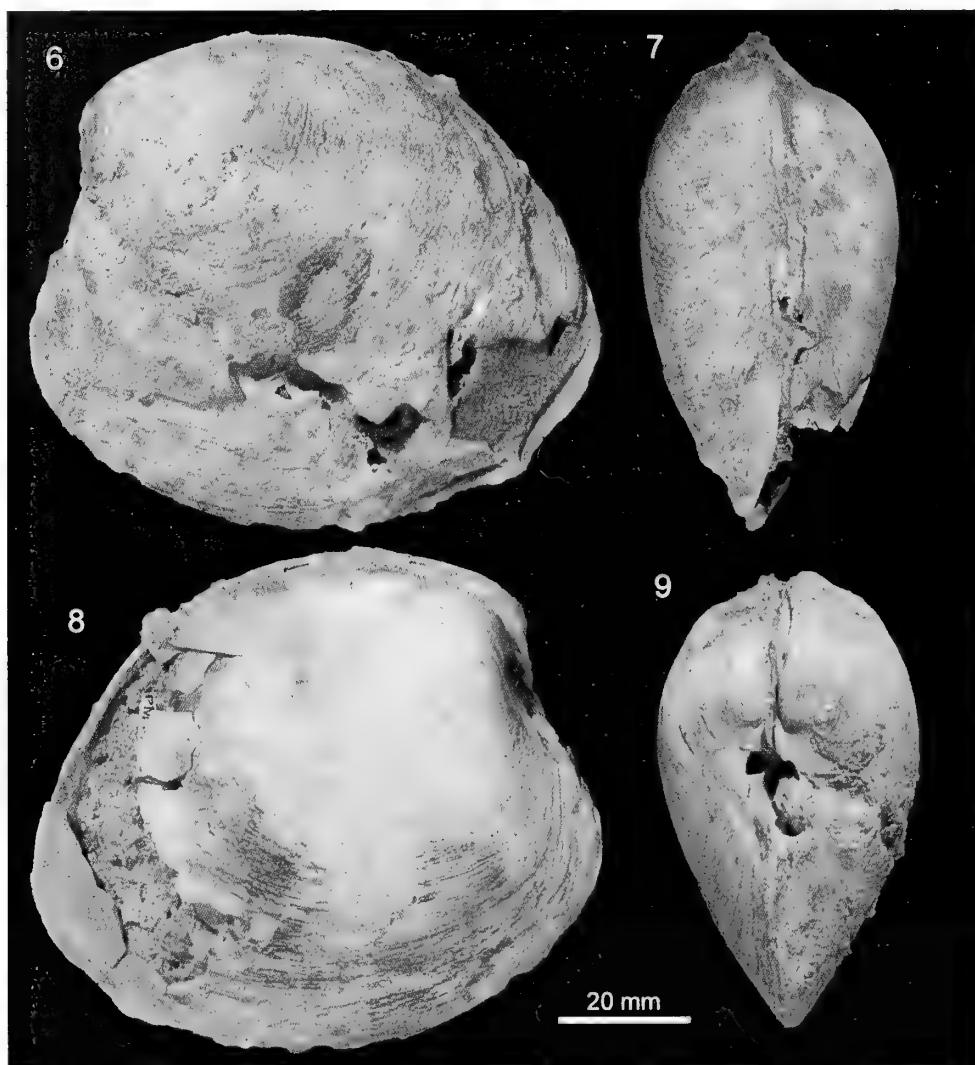
SYSTEMATICS

Family Vesicomyidae Dall and Simpson, 1901

Genus *Wareniconcha* Cosel and Olu, 2009

Type Species: *Vesicomya guineensis* Thiele and Jaeckel, 1931; Recent, from ca. 2500 to 4000 m depth on the West African continental margin (Cosel and Olu, 2009).

Remarks: Cosel and Olu (2009) included only the type species in *Wareniconcha*. In a subsequent review of vesicomyid species, Krylova and Sahling (2010) considered also the following species as belonging to *Wareniconcha*: *Vesicomya compressa* Prashad, 1932, *Vesicomya cretacea* Smith, 1906, *Vesicomya lepta* Dall,



Figures 6–9. *Wareniconcha mercenarioides* new species; paratype I (NMP-2148). **6.** Left valve. **7.** View on posterodorsal margin. **8.** Right valve. **9.** View on anterior side.

1895, *Vesicomya ovalis* Dall, 1895, and *Vesicomya winckworthi* Prashad, 1932.

***Wareniconcha mercenarioides* new species** (Figures 1–9)

Diagnosis: Large and inflated *Wareniconcha* species that is about as high as wide, with a broad ligament nymph plate.

Description: Large, inflated shell, up to 12 cm long, slightly longer than high; umbones large, blunt, strongly prosogyrate; shell surface sculpture by fine, regular growth increments; anterior part short, somewhat pointed; posterodorsal margin broadly and evenly rounded, with angular transition to the equally broadly and evenly rounded ventral margin. Right valve with strong cardinal 1 radiating anteriorly, positioned anterior of umbo, cardinal 3a thin and short, positioned just anterior of umbo, cardinal 3b short,

moderately strong, pointing posteriorly. Left valve with strong and elongate cardinal 2a subparallel to dorsal margin, cardinal 2b strong, quadrate, just beneath umbo, cardinal 4 thin, elongate, pointing posteriorly; nymph plate long and broad.

Type Locality: The Liog-Liog seep deposit.

Type Material: Holotype: NMNS PM 28168, articulated specimen (length 11.3 cm, height 9.7 cm, width 6.5 cm); **Paratype 1:** NMP-2148, articulated specimen (length 11.3 cm, height 10.1 cm, width 5.7 cm); **Paratype 2:** NMNS PM28169, disarticulated specimen (length ca. 12 cm, height, ca. 10 cm) consisting of incomplete right valve.

Distribution and Habitat: Pliocene methane-seep carbonates at Liog-Liog Point, Tabango municipality in Leyte, Philippines.

Etymology: For its shell shape resembling the venerid genus *Mercenaria*.

Remarks: *Wareniconcha mercenarioides* differs from all species assigned to *Wareniconcha* (see list above in the remarks about *Wareniconcha*) by being larger, more inflated, and being roughly as wide as high, whereas all other *Wareniconcha* species are oval in an anterior-posterior direction. Furthermore, *W. guineensis*, *W. compressa*, and *W. lepta* have a narrower hinge plate than *W. mercenarioides*.

Many of the accompanying bivalve species at the type locality belong, or are very similar to, extant species from vents and seeps in Japanese waters and especially in the Okinawa Trough (including, for example, *Bathymodiolus securiformis* (Okutani et al., 2004), *Archivesica soyoae* (Okutani, 1957), *Archivesica similaris* (Okutani et al., 1997), *Archivesica kawamurai* (Kuroda, 1943), and *Pliocardia kuroshimana* (Okutani et al., 2000); TK and SK, unpublished). Therefore, we anticipate that *Wareniconcha mercenarioides* or a very closely related species may still be extant somewhere around the Indo-West Pacific.

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